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A CLASS BOOK OF BOTANY

BY

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WITH OVER TWO HUNDRED ILLUSTRATIONS SPECIALLY DRAWN FOR THE WORK

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PREFACE

MANY years' experience in preparing students for the examinations in this subject of London University and of the Board of Education has impressed us with the need of a *single* work that shall deal fully with all their requirements. As is well known to teachers, the study of 'types' in a not too exclusive manner constitutes the guiding principle of all modern teaching in Elementary Botany, exemplified for instance in the syllabus issued by the Senate of London University and the Board of Education respectively. Accordingly, our work is based upon this principle, and the 'types' which we have chosen, as suitably and conveniently illustrating Phanerogamic Morphology, are those which our experience in the laboratory has taught us are suitable in most respects for the practical study of them by students; and we believe that other teachers will find them equally applicable to the purposes of their classes in the subject.

No single plant-type, however, can illustrate equally well the typical structure of all the organs of plants; but as far as the types chosen are adapted to do so, we have described them with sufficient fullness, and have only considered as far as necessary for a clear understanding of the whole, the remaining features of the type which do not represent a typical condition. In dealing with the minute structure and development of the floral organs especially, we have thought it advisable to depart from a too rigid adherence to the single type principle, and we have there-

fore written a general account illustrated by several plants, each of which shows more or less typically the particular feature it is used to illustrate. In some few instances, as for instance in using the flower of *Inula* to illustrate the development of the floral organs, we have preferred to substitute it for a more typical one, in view of the practical utility in using composite flowers for this purpose.

In the treatment of the physiological section, we have endeavoured, both in the text and in the illustrations, to render it possible for the student to work practically at experiments on plant physiology, and we trust that teachers will find this section of value to them in conducting practical classes in this important and interesting branch of botanical study.

In the final portion of the book, which is devoted to the study of Systematic Botany, we have endeavoured to deprive this part of the study of some of its dreariness, by making the facts real and apparent through the agency of copious illustrations of floral diagrams, of the forms of leaves, of fruits, of dissections of flowers, and of special floral modifications. We are sure that these will be appreciated by teachers and students alike; and if students will supplement the use of them by an appeal to nature, the false idea that Systematic Botany is dry will be quickly dispelled.

All the figures which illustrate the work have been specially prepared for it, and in each case have been sketched from the actual preparations. One of our objects in so doing is, by the example thus set, to encourage students to sketch and to otherwise record their own observations, for no methods have been used in the preparation of the specimens from which the illustrations have been drawn, other than the very simplest, such as any student should be taught in any good class.

This work is primarily intended to meet the requirements of students who are preparing for the Intermediate Scientific B.Sc. and Preliminary Scientific M.B. examinations of the London University, or for the Advanced Stage examinations of the Board of Education. But students who intend sitting for other examinations in the subject, as, for instance, those for the Natural Science Tripos of Cambridge and Oxford, for the Faculty of Science of Edinburgh and Glasgow Universities, for the Oxford and Cambridge Higher Locals, for the Indian Civil Service, and for the LL.A. of St. Andrews, will find that the contents of the book embrace a considerable portion of the work required.

We desire to record our best thanks to Miss Gertrude M. Smith for much kind help in the preparation of some of the illustrations, and for valuable aid in reading parts of the proofs in Part I; and to Mrs. Maslen, who kindly helped us in reading the proofs of Parts II–IV. To Mr. Maynard Upfield, one of Mr. Mudge's students, we have also to express our thanks for his kindness in preparing a beautiful series of sections showing the development of lateral roots, from which our illustrations on root structure and development have been derived.

While both authors accept their responsibility for the correctness and arrangement of the work as a whole, Mr. Mudge is mainly responsible for the preparation of Part I, dealing with the structure and life-history of the types, and Mr. Maslen for the remainder.

G. P. M.
A. J. M.

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BOTANY

PART I

THE STRUCTURE OF PLANT-TYPES

CHAPTER I

INTRODUCTORY

Botany is one of the branches of a great science called **Biology**, which seeks to study the structure and activities of living things. Whatever has to do with life, from Man and his social institutions at the top of the scale, down to microscopically minute and exceedingly simple bacteria at the bottom, is embraced within the range of its studies. Living things may be divided into two great classes, animals and plants. **Botany** is concerned with the study of the latter class, and **Zoology** with that of the former. At first sight, nothing appears more natural or more obvious than this division of the living kingdom; and without doubt it is easy enough to distinguish between the higher animals and plants, for animals as a whole are characterized by the possession of an alimentary canal in which the digestion of food goes on, by the ingestion of *solid* food of a highly complex chemical nature, by their power of locomotion, and by their irritable response to external stimuli; while plants, on the other hand, possess no alimentary canal, do not ingest solid food, but take the food-substances in over the general surface of their body, in the form of gases and liquids, which are of a very simple chemical nature; they are not locomotor, and cannot therefore move from place to place, but remain fixed to one spot throughout the whole of their existence, and neither do they as

a class exhibit any response to external stimuli. These are negative characteristics, but plants are also distinguished from animals by at least two positive characters, for their green colour is due to a substance called **chlorophyll**, and its presence is nearly universal throughout the plant kingdom ; in fact, for practical and philosophical purposes, we may say that it is universally present ; for the only group of plants, i. e. the fungi, in which it is absent, are to be regarded as descended from green plants. The other character of a positive kind is the nature of the material to which the rigidity of plants is due, and by means of which its substance is divided up into a number of microscopic compartments, called cells. This substance is chemically allied to starch, though physically different ; it is known as **cellulose**, and no plant exists in which it is not a constituent element, either throughout the whole or a part of its existence.

The distinguishing characters thus indicated are easily discerned if we compare the higher animals and plants ; but when we range over the living kingdom, and especially when we study some of the lower forms, these characters no longer hold as hard and fast lines of distinction between the two great classes of animate beings. For there are animals, like the tape-worm, which do not possess any alimentary canal and do not ingest solid food, but imbibe it in a liquid form through the whole surface of their body. And conversely, although there are no animals which are capable of forming their tissues out of the chemically simple substances like carbon dioxide and mineral nitrates, as green plants can, there are nevertheless green plants, like *Drosera* (sun-dew) and *Nepenthes* (pitcher-plant, infra, p. 424), which possess the power of digesting solid food and of building up their tissues out of complex proteids, as animals do. And the great group of fungi, like animals, needs organic substances as food, and thus differs from the green-plants. With respect to locomotion, there are many animals such as corals and oysters which are as fixed throughout life as the oak-tree or other plant ; and conversely, there are plants whose reproductive cells are motile, as we shall later learn in detail, moving from place to place by their own movements. Similarly with regard to the other apparent difference between animals and plants, i. e. that of reflexive response to external stimuli ; for there are plants which react to the external influence of light, temperature, chemical stimuli, electricity, touch, and gravitation, in as decisive a manner as animals do, though by a less complex mechanism (cp. chap. XXIV, pp. 466–475).

When we consider the two almost diagnostic features of the plant kingdom, i.e. the possession of chlorophyll and cellulose, we find that it no more serves as an absolute boundary-line between the two classes of living things than do the other characters. For there are some animals, like *Hydra* (fresh-water polype), and some flat-worms, in which chlorophyll is present, and there is reason to believe that it plays an important part in their economy. Cellulose can be easily demonstrated to be present in the leathery integument of some sea-squirts (*Ascidia*), so that this distinction, as an absolute one, breaks down also.

Furthermore, low down in the scale of life, there are some organisms which at one period of their existence are indubitable animals and at another equally indubitable plants. The *Myxomycetes*, a class to which the 'Flowers of Tan' belong, in the vegetative (feeding and growing) stage of their existence, creep about as masses of a jelly-like substance called protoplasm—a substance which is the physical basis of all living things—and ingest solid food of an organic nature; thus at this stage they are animals in virtue of the power of locomotion and the ingestion of solid food of a proteid kind. But in the reproductive phase of their history, they form sporangia (spore-cases)—the wall of which is of cellulose—and spores, in a manner which is characteristic of plants and not animals. And there are other lowly organisms of a like nature, which stand on the borderland of the animal and plant kingdoms, and can be said neither to be the one nor the other.

There is, therefore, no absolute boundary-line between the two great classes of living things; for as we trace them downwards they converge to a condition which belongs to neither, but is common to both.

This leads us to seek an explanation of these facts. At present, no intelligible interpretation can be placed upon them, other than the one that the animal and plant kingdoms have arisen from a common ancestry. From this primitive stock, plants probably evolved along one line, and animals along another.

The Great Divisions of the Plant Kingdom.

At first sight it is apparently a hopeless task to endeavour to reduce to order the multitudinous forms of plants. The indefiniteness and immensity of their variety is appalling, and is sufficient to turn back the most ardently courageous student, if he ventures to attack the problem in the wrong way. The dry and uninteresting description

of species, consisting for the most part of records of minute and apparently trivial details, that characterized the works of the older botanists, may appear to the uninitiated student to be so much record of pedantic labour; but they have played their part in producing order out of chaos, and it is not too much to say that their work was an absolutely necessary preliminary to the discovery of evolution. As a matter of fact, the history of science demonstrates that no detail is so trifling as to have no significance, in any philosophical survey of a given range of inquiry.

One of the most obvious distinctions between plants, if we study them with sufficient care, is that some of them bear flowers, while others do not. Plants like ferns, mosses, and sea-weeds, do not develop any organs which are exactly comparable to flowers, and so the plant kingdom is divided into the **Flowering plants** and the **Flowerless plants,** or as they are technically known, the **Phanerogams** and **Cryptogams** respectively.

Let us consider the Phanerogams first. When we examine the flowering plants, we find that they may be divided into two groups: for in the one, the seeds are enclosed in a seed-case, while they are not in the other; or in other words, and to take a slightly earlier stage in the development of the flower, in the one class the flower possesses an ovary[1], while in the other it does not. So the Phanerogams are divided into two subdivisions, **Angiosperms,** or those plants in which the seed is enclosed, and **Gymnosperms,** or those in which the seed is naked or unenclosed. To the Angiosperms belong all the more familiar plants, such as the rose, the primrose, the lily, the geranium, the elm-tree, the horse-chestnut, &c.; and to the Gymnosperms, the fir, the larch, the pine, the maiden-hair tree, and the cycads.

If we study the angiospermous plants, we shall soon learn that they may be divided into classes called the **Dicotyledons** and the **Monocotyledons.** The majority of flowering plants belong to the Dicotyledons, and we may for the purposes of comparison between the two classes take a bean-plant and a primrose as examples of Dicotyledons, and a lily or hyacinth and the Indian corn-plant as examples of Monocotyledons. If we grow some seeds of the bean-plant and Indian corn, and allow them to germinate, we shall see that on the young plant which arises from the bean-seed there are

[1] The seed-case is the ripened ovary.

two seedling leaves or **cotyledons** (Fig. 3) as they are called. These seedling leaves are better seen in the maple or beech seedling than in the bean, because in them they are more distinctly leaf-like. In the seedling of the Indian corn only one such leaf or cotyledon is present. Hence the separation of flowering plants into dicotyledons or those plants with two cotyledons on the seedling, and monocotyledons or those with one.

This difference, however, is correlated with others; for if we examine the leaves of the bean-plant or any other dicotyledon, we shall see that the veins form a network (Fig. 1), while in the leaf of the Indian corn or lily, or any other monocotyledon (Herb Paris excepted), the veins run parallel with one another and do not form a network (Fig. 225, IV). In Dicotyledons, the number of parts (sepals, petals, &c.) present in the flower are either two, four, or five, while in Monocotyledons they are either three or some multiple of three. There are other differences between these two classes, but as they are concerned with the internal anatomy of the plants, we shall defer their consideration.

For our immediate purpose we may divide the flowerless plants or **Cryptogams** into the **Vascular Cryptogams** and the **Cellular Cryptogams**. The former are characterized, like the Phanerogams, by the possession of certain strands running through the length of the stem and roots, and outwards into the leaves, and which we may speak of for the present as **vascular strands**. They are definite channels for the transmission of food-materials taken up by the roots, and for the passage of elaborated food-substances manufactured by the leaves. The Cellular Cryptogams do not possess these strands.

As types of the Vascular Cryptogams we shall study *Selaginella* and the fern, and as types of the Cellular Cryptogams, a liverwort, a moss, and certain algæ and fungi.

We may briefly summarize the relation of the great groups to one another thus:—

Phanerogams	**Angiosperms**	Dicotyledons	Sunflower, *Inula*, *Caltha*, bean-plant, elm, mare's tail, water-lily, &c.
		Monocotyledons	Maize-plant, *Yucca*, *Potamogeton*, lily, &c.
	Gymnosperms		Pine, larch, maiden-hair tree, cycads, &c.
Cryptogams	**Vascular Cryptogams**		*Selaginella*, fern, &c.
	Cellular Cryptogams		Mosses, liverworts, Algæ and Fungi.

Modes of Branching of Stems and Roots.

We shall have to refer later to the different modes of branching which the stems and roots of plants exhibit, and it will be well to give a general account of the chief systems before passing on to consider our types.

When a stem divides at its apex into two or more branches, which at first grow equally vigorous, and each of these in their turn branch in the same manner, we apply the term **dichotomy** if there are two branches, and **polyotomy** if there are more. If one of the two branches at each bifurcation (two-pronged) grows stronger than the other, there results what appears to be a main axis formed by the stronger of the two branches, with lateral axes formed by the weaker branches, arising from it; this is called a **sympody.** Of this we may have two varieties: in one the stronger branch always arises on the same side, when the main axis appears to bend always in one direction and to assume a form like the handle of a shepherd's crook; and in the other it arises alternately right and left, when the main axis may be nearly straight or more or less zig-zag in form. In the former case we call it a **helicoid dichotomy,** and in the latter, a **scorpioid dichotomy.** Dichotomous branching is uncommon and only rarely occurs in leafy shoots; but it is common among the Cryptogams, and we shall see later that the thallus of *Pellia* and of *Fucus*, and the roots of *Selaginella* branch in this manner.

When the main axis continues to grow at its apex, and produces branches as lateral outgrowths behind, which do not grow as vigorously and therefore do not become as large as the parent axis, we term it a **racemose** or **monopodial** mode of branching (Fig. 161, I to VIII), p. 299.

If the lateral branches which arise grow more vigorously and branch more profusely than the primary axis *above* their point of origin, we call it a **cymose** system of branching. If all the lateral branches in a cymose system grow equally vigorously there results a resemblance to a dichotomy or a polyotomy, according as there are two or more lateral branches; such a cymose branching is called a **false dichotomy** or **polyotomy.** In many cases a false dichotomy can only be distinguished from a true dichotomy by a knowledge of the development of the branches, for the latter system only arises by the division of the apex of the primary axis into two, whereas the former arises from lateral branches growing out behind the apex; the resemblance to

a true dichotomy is produced by the insignificant development of the main axis *above* the origin of the lateral members, and of the vigorous growth of these. If, of the lateral branches, one only grows vigorously and the other does not, there is produced an apparent main axis, but in reality composed of the successive vigorous lateral axes, the less developed axes appearing as lateral branches on the apparent main axis. This results in a sympody, and in the same way that a dichotomous sympody may become helicoid or scorpioid (supra, p. 6), so too may a cymose system become a **helicoid cyme** or a **scorpioid cyme**, dependent upon the development of the stronger branch always on one side or alternately right and left respectively. And here, too, the difference between these two forms of cymes may be distinguished from the *same* forms of dichotomy, only by a knowledge of the mode of their development.

Phyllotaxis.

By the term **phyllotaxis** we understand the mode of arrangement of the leaves upon the stem, in relation to the interval that exists between any two of them. If we examine a dead-nettle (*Lamium album*) we shall find that the leaves are arranged on opposite sides of the stem ; that is, in passing from the insertion of one leaf to that of another, we shall pass half way round the circumference of the stem. The interval between the insertions of the leaves is thus one-half the circumference of the stem ; we speak of this as the **divergence of the leaf**, and in this case we say the divergence is $\frac{1}{2}$. If we were to examine the shoots of some other plants we should find that the interval was $\frac{1}{3}$; this we can determine, by starting to pass round the stem from the point of insertion of a given leaf until we reach a leaf inserted vertically above it. In this particular instance we should find that in passing once round the stem we should have to pass the insertions of three leaves before we reached that of one immediately over the one from which we started. Thus the divergence is $\frac{1}{3}$, the numerator representing the number of times we pass round the stem, and the denominator the number of leaves passed, including the one at which we stop, but not the one at which we commenced. The next divergence is $\frac{2}{5}$, that is, in passing twice round the circumference of the stem we pass through the insertions of five leaves. And so on for the other divergences.

The commonest divergences are :—

$$\frac{1}{2}, \frac{1}{3}, \frac{2}{5}, \frac{3}{8}, \frac{5}{13}, \frac{8}{21}, \frac{13}{34}.$$

This series is easy to remember, for the sum of the numerators and of the denominators, of any two given fractions, is the fraction expressing the next highest divergence.

CHAPTER II

DICOTYLEDONS

HERBACEOUS TERRESTRIAL PLANTS

THE SUNFLOWER (*Helianthus annuus*) and BEAN-PLANT (*Phaseolus multiflorus*).

1. External Characters.

(A.) The Shoot and Root.

The sunflower and bean-plant may be taken as representing two fairly typical **herbaceous dicotyledons**; the former is very typical in the minute structure of its stem, and the latter in that of its root; while in both the flower is structurally adapted to special conditions.

They are called herbaceous plants because they remain green externally the whole of their life—their stems never become invested in a brown corky layer, except at their base towards the end of the year—and they never form a great quantity of wood internally. Like most herbaceous plants, they are also **annuals**, that is, they flower in the first year of their existence and then die, and thus have to be raised anew each year from seeds.

If we examine a fully developed and flowering sunflower, we shall note that above ground it consists of a stout, more or less cylindrical, vertical stem, terminated at its apex by a large disc-like aggregate of flowers, and bearing at intervals along its length large, more or less heart-shaped leaves. At the base of the stem the leaves are **opposite**, i.e. inserted on the stem opposite to one another, but higher up, they **alternate**, i.e. the leaves are inserted at different levels; the transition between the opposite and alternate arrangement is gradual. The leaves are further arranged in such a manner that the oldest are at the base, and the youngest at the apex of the stem, so that as we pass from the base upwards, we pass successively through younger leaves; in other words, the order of succession in space

is the order of succession in time: this arrangement is called **acropetal succession.** The stem does not branch except at its upper portion, and then but sparsely; each branch, which itself bears leaves and is terminated by a flower, is called a **shoot**, and it arises in the axil of a leaf, i. e. in the angle formed by the leaf with the stem. All shoots arise in the axil of a leaf, so that, however much they may be modified, as in the gorse (Fig. 10) and hawthorn (Fig. 8), where they have become converted into spines, their morphological[1] nature may be inferred from their relation to the leaf; moreover, all shoots bear leaves, so that, however unlike a stem any member of a plant may appear to be, if it bears leaves, even though they are reduced to mere scales, it must be regarded as the morphological equivalent of a shoot.

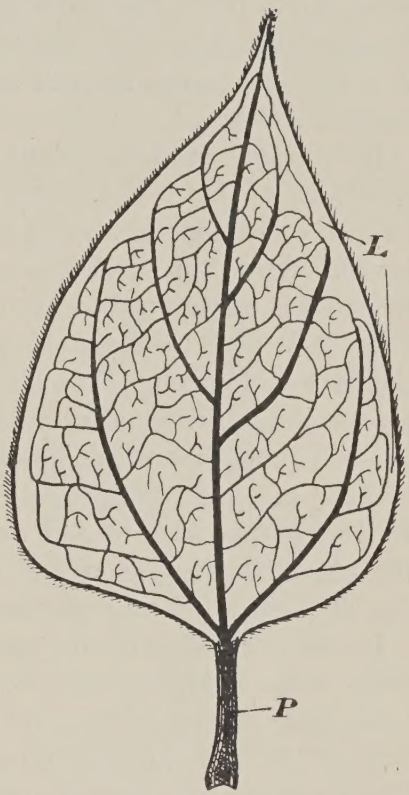


FIG. 1. A Sunflower leaf, showing division into lamina or blade (L) and petiole or leaf-stalk (P). The margin of the leaf is ciliated, i. e. bears numerous small hairs. The leaf also shows a reticulate or branching venation.

In its lower portion the stem is striated and cylindrical, but above, where the lateral branches are developed, it is unstriated and more or less polygonal in form. Along its whole length it is covered with stiff hairs, which are, morphologically considered, merely outgrowths of the outer covering or epidermis of the stem. **Prickles**, such as occur on the wild rose (Fig. 8), are modified hairs, since like them they are merely epidermal outgrowths; and they differ from the **spines** of the hawthorn and the **thorns** of the sloe (Fig. 9), which are modified branches and arise from tissues which lie deeper than the epidermis, and, like all shoots, within the axils of leaves.

The leaves (Fig. 1) are very large, and each consists of a broad,

[1] **Morphology** is the **Science of Form**, and since Form depends on structure, we may define Morphology as the study of structure. Any organs which have the same structural relationships and origin, however different they may appear to be, are regarded as morphologically equivalent.

heart-shaped blade or **lamina** (L) attached to the stem by means of a long stalk or **petiole** (P), cylindrical in form, with its upper face flattened or slightly concave. The lamina is **simple**, i. e. not divided into smaller leaflets, and it obviously has two surfaces, an upper directed towards the stem, and an under directed downwards and away from it; leaves which have two obvious surfaces, and are arranged in a horizontal plane, are said to be **bifacial** in distinction to cylindrical leaves, such as those of the stonecrop, which are called **centric** leaves.

If we pull a sunflower-plant from the ground and examine the root, we shall find that it has a main axis continuous with that of the stem, and which bears a number of lateral roots, upon which others may be borne. A root in which the main axis is the continuation of that of the stem is called a **tap-root**, in order to distinguish it from a **fibrous root**, such as is possessed by grasses, in which many roots arise from the base of the stem. The lateral roots, like the leaves upon the stem, are formed in acropetal succession. A careful examination of the rootlets will show that a little behind the apex of each there arises a great number of small, filamentous structures, the **root-hairs** (Fig. 3), to which the particles of soil are very intimately attached; these are the absorptive organs of the root, which absorb the mineral matter dissolved in the water in the soil.

If now we compare the root and the stem, we shall see that they differ in the following features: the apex of the root grows downwards, while that of the stem grows upwards; the lateral members (rootlets) of the root are like those of the principal member, while the lateral members (leaves) of the stem are unlike the principal member. There are other differences between stem and root, but these we shall consider later.

The stem of the bean is a slender climbing one, ascending from the ground by twisting itself round any support that may be near, and always in the same direction. In section it is oval in form, and its surface is marked by longitudinally-directed striæ, which by their spiral twist indicate that the substance of the stem has itself become twisted. At long intervals it bears alternately arranged leaves, with long petioles and broad blades (Fig. 2). At its insertion upon the stem, the petiole bears on either side a small, lance-shaped, leaf-like appendage, called a **stipule** (S), and its upper surface is traversed by a deep groove. The lamina or blade (L) is very large, and is divided into three leaflets, of which one is terminal and the remaining

two lateral in position upon the petiole. Each leaflet is broadly egg-shaped in form, with the narrow end tapering, at first suddenly, then more gradually to a point; the margin of each leaflet is **entire**, i. e. not indented by teeth or crenations, and **ciliated**, that is, fringed by small hairs. A single principal vein traverses each leaflet from base to apex, and from it there spring a number of lateral veins which pass outwards to the margin, and then turn forwards towards the apex. Held towards a strong light, it can be seen that the substance of the leaf between the lateral veins is traversed with a close-set meshwork of small veins, derived from the branching of the lateral ones. The formation of a network of veins in the substance of the leaf, by means of which the larger ones become connected, is very characteristic of a class of plants called **Dicotyledons**—a name given them because the seedling leaves or **cotyledons** are always two in number. This particular type of venation is called **reticulate**. The leaves of the sunflower and bean are alike in that they both have a reticulate venation, but they differ in that in the former there are several principal veins (**multicostate venation**), and not one (**unicostate venation**), as in the latter.

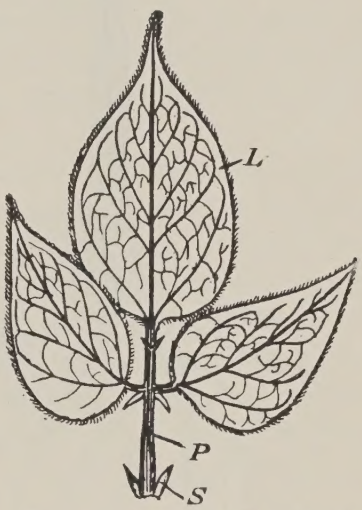


FIG. 2. A compound leaf of the Bean-plant, showing the division of the lamina (L) into three leaflets, attached to a common petiole or leaf-stalk (P). The petiole bears leaf-like appendages, called stipules (S).

In the axil of every leaf a flowering shoot is borne, which bears a long raceme of showy, red flowers. Leaves in the axils of which a flowering branch arises are called **bracts**; but no morphological significance is indicated by such a name, for as we see, the bracts here are simply the ordinary vegetative leaves; nevertheless, in some instances, the bracts differ in form and texture, but not in position, from the vegetative leaves.

Upon the flower-stalk or **peduncle**, there are borne a number of small leaf-like structures, each of which consists of a median, larger lobe, and two lateral smaller lobes. These are usually distinguished as **bracteoles**, and in the axil of each a shortly-stalked flower arises. The bracteoles, morphologically considered, are modified leaves; and the pedicels or stalks of each individual flower are,

therefore, modified branches, since they arise in the axils of leaves. If this is so, then the parts of the flower, the sepals, petals, stamens, and carpels are modified leaves, since they arise upon a branch; and we may regard each flower as a modified shoot, in which the leaves have become modified for reproductive purposes.

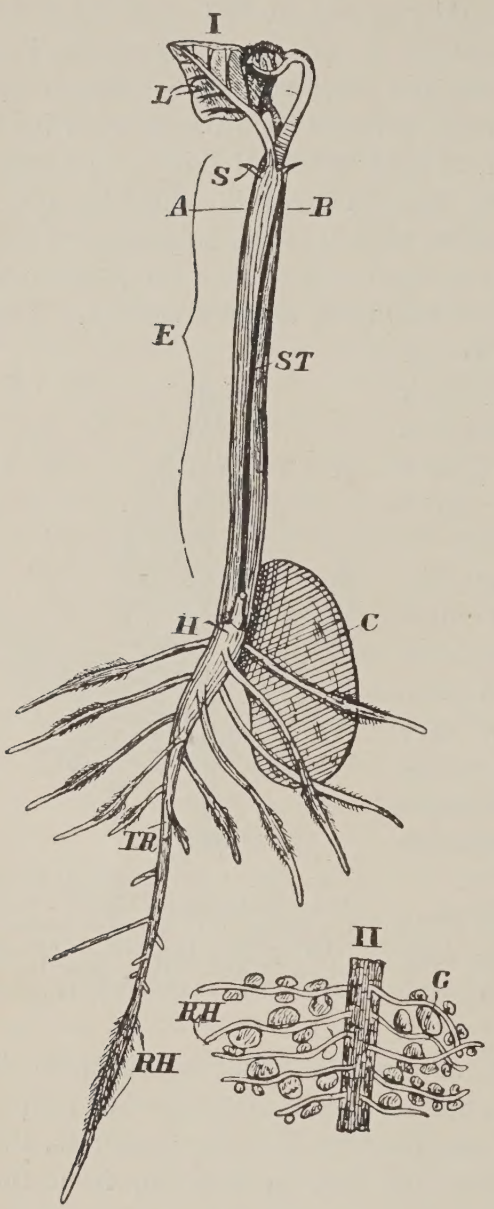


FIG. 3. I. A seedling Bean-plant. C=cotyledon; E = epicotyledonary portion; H = hypocotyledonary portion; L=leaf; S=stipule; ST=stem; TR=main axis of root; A—B=plane of section of Fig. 32. II. A portion of root, from the root-hair bearing region just behind the apex, magnified 15 times to show the root-hairs and the attachment of particles of soil (G) to them.

The root of the bean (Fig. 3), like that of the sunflower, is a tap-root. The two roots in all essential features are identical, but that of the bean exhibits in a more marked manner the arrangement of the lateral roots and rootlets in four longitudinal rows. This arrangement of the lateral roots is connected with their mode of origin from the central tissues within the parent root, and will be further considered when we study the minute structure of the root.

A superficial examination of the root of a well-grown plant (not a seedling) will reveal the fact that it bears a number of small, globular enlargements: these are not of any morphological importance, though physiologically[1] they play an important part in the economy of the plant. They are merely swellings of the ground-tissue of the root, which have been produced by the entry into it of

[1] **Physiology** is the **Science** of **Activities** or **Functions.**

a mycelial (filamentous) fungus ; this latter gains its entry by the secretion of a ferment capable of dissolving any portion of the substance of the root with which it comes in contact, and thus it gradually dissolves its way into the tissues of the root. But the entry of the fungus opens the way for the admission of another, which possesses the power of taking up the free nitrogen of the atmosphere and passing it on to the plant. Nitrogen is an important food constituent, and it is only plants of the pea and bean kind which can thus obtain it direct from the plentiful store in the atmosphere ; other green plants, like the sunflower, which have no tubercles upon their roots, can only utilize it when it is in combination with other elements, as in the mineral matter (calcium nitrate, &c.) present in solution in the soil. The formation of the nodules upon the root is in some way connected with the entrance of the latter fungus, which is a member of the bacteria.

An examination of the general habits and form of the bean-plant and the sunflower thus demonstrates that a fully developed green plant is composed of a number of anatomically[1] different parts or **members**: a **root**, **stem**, and **leaves**. A root is always characterized by the fact that it grows downwards in obedience to the force of gravitation and that it bears lateral members similar to itself ; while a stem grows upwards in opposition to gravitation and bears lateral members, the leaves, unlike itself. A shoot consists of a stem plus the leaves, and always arises from the parent shoot in the axil of a leaf. The point of insertion of the leaf upon the stem is called a **node**, and the interval along the stem between two nodes an **internode**. Some of the shoots have very short internodes and bear modified leaves, the function of which is the production of seed ; these are the flowers. A leaf when complete consists of three parts, a lamina or blade, a petiole or stalk, and a leafy appendage or stipule ; in the sunflower the leaf is not structurally complete, for the stipules are absent, and in many plants so also is the petiole.

The stems of the sunflower and the bean-plant are vertical, but there are many stems which creep along or just beneath the surface of the ground, giving off roots from their lower surface, and leaves from their upper. Those which grow underground and send up shoots at intervals, as in the bracken fern, polygonatum, and iris

[1] Anatomy is the study of gross structure.

(Fig. 4), are called **rhizomes.** Shoots which grow along the surface of the ground, producing at intervals roots and foliage leaves, are called **stolons,** as in the creeping buttercup and strawberry. Some underground stems thicken considerably at their terminations and form more or less rounded masses called **tubers**; the potato-plant affords a good instance of this (infra, p. 18, Fig. 12).

In many plants, the lateral branches and the leaves become very

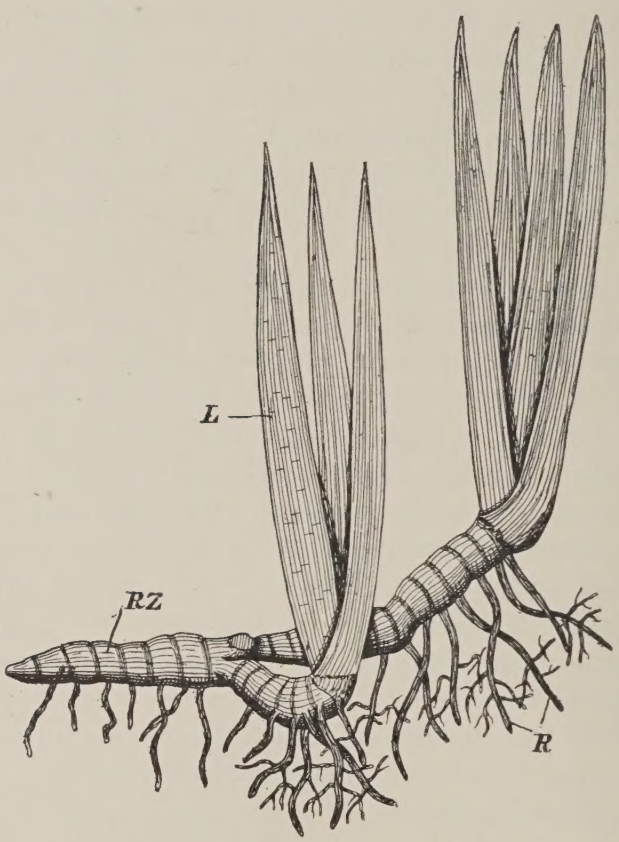


FIG. 4. An Iris-plant much reduced, to show the branching underground stem or rhizome (RZ), with the leaves (L) of the current year borne near the apex of the branches, and the scars of past years' leaves at intervals along their length. R=roots.

much modified in correlation with the assumption of new functions. In the bean, the climbing-organ is the main axis or stem itself; but in the Virginian creeper, the grape vine, and the sweet pea it is a tendril. The tendril in all three instances serves the same physiological purpose, and they are, therefore, said to be **analogous** members; but the tendril in the creeper and the vine are not

morphologically the same as that of the pea, so that the tendril of the latter is not **homologous**[1] with those of the two former.

If we examine the tendril of the Virginian creeper (Figs. 5, I, & 6), we shall find that it is a branching organ, which arises from the apparent main axis opposite the insertion of a leaf (F & LS); it also bears small scale-like leaves (L), which arise at different parts of the tendril and in the axils of which lateral tendrils arise. The fact that

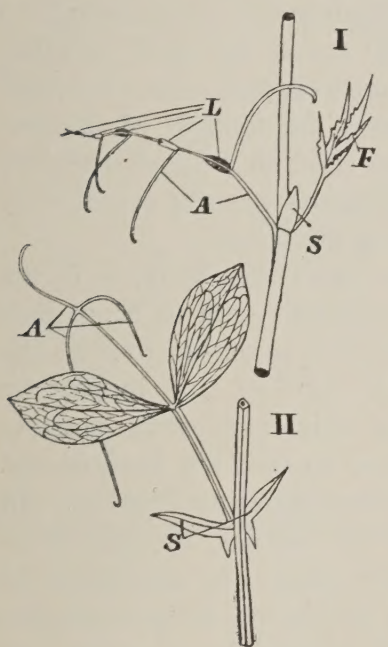


FIG. 5. I. A portion of the stem of the Virginian Creeper, showing the stem-tendril. A=tendril; F=foliage leaf; L=scale-like leaves; S=stipules. II. A portion of the stem of the Everlasting Pea showing leaf-tendrils A. S=stipules.

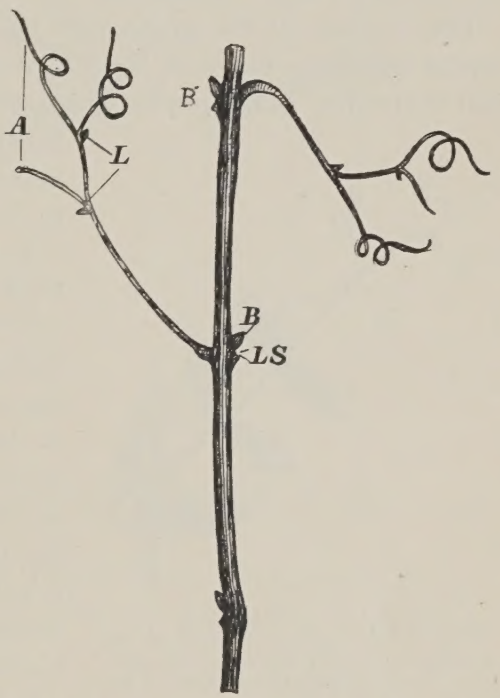


FIG. 6. A portion of the stem of the Grape Vine, showing stem-tendrils. A=tendril; B=bud; L=scale-like leaves; LS=leaf-scar of fallen leaf.

the tendril bears leaves shows that it is, morphologically considered, a modified stem. But if this be its nature, it should itself arise in the axil of a leaf, instead of which it arises opposite the insertion of one. To intelligently understand this morphological interpretation of the tendril of the Virginian creeper and grape vine, the student must have some knowledge of the modes of branching of plant-stems,

[1] **Homology** expresses the idea that certain organs, when compared, are seen to be morphologically identical, and **Analogy** that they are morphologically different, but physiologically the same, i. e. serving the same physiological purpose.

and he should refer to chap. I, p. 6, and study the nature of the sympodial variety of dichotomous branching. He will then see that the shoots of the creeper and the vine are sympodia, in which one of the two branches formed at each bifurcation is converted into a tendril, while the other becomes a constituent part of the apparent main axis. Every third leaf bears no tendril opposite to it (Fig. 6), and this must be interpreted by assuming that each podium (the parent axis of each bifurcation) bears alternately one or two leaves.

The tendrils of the grape vine (Fig. 6) are of the same morphological nature as those of the Virginian creeper, and since they both also serve the same physiological purpose, the tendrils of the one plant are said to be **homologous** and **analogous organs** respectively to those of the other.

FIG. 7. A compound leaf of the Sweet Pea plant (*Pisum sativus*), showing the broad stipules at the base of the petiole, two pairs of unmodified leaflets above, and the leaflets modified into tendrils above these.

In the pea (Figs. 5, II, & 7) the tendril is clearly seen to be in part composed of the continuation of the petiole of the leaf, and in part by filaments which occupy the position of leaflets, so that the tendrils are modified leaf-stalks and leaflets. In some of the vetches, the petioles of the earlier leaves are terminated by a leaflet, but in the older leaves, the leaflet is replaced by a tendril. In *Cobœa scandens*, a common garden climbing plant, not only is the terminal leaflet of the earlier leaves represented in the later ones by a tendril, but also some of the lateral ones. In such instances the tendrils are modified leaflets. Tendrils are therefore either **stem-tendrils** as in the vine and creeper, or **leaf-tendrils** as in the pea and *Cobœa*.

In the hawthorn (*Cratægus*, Fig. 8, II) there is borne in the axils of most of the leaves a spine, and careful examination will reveal the presence of one or two minute scales upon it; its position in the axil of a leaf shows it to be a modified branch, and the scales upon it are, therefore, of the morphological nature of leaves, so that the spine as a whole is a modified shoot. In some species of hawthorn the spines have become very much enlarged and form thorns, upon

which ordinary vegetative leaves are borne. The thorns of the sloe (Fig. 9) are of the same nature as those of the hawthorn, but the leaves upon it are not so much reduced and within their axils rudi-

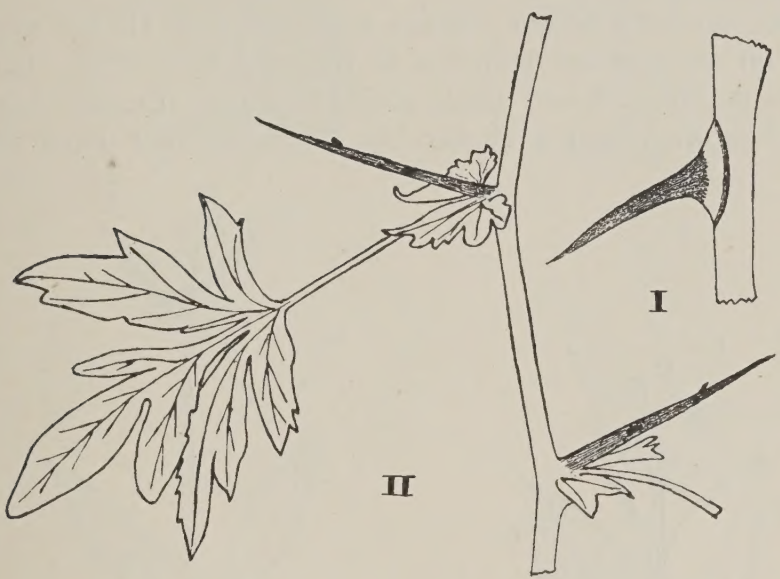


FIG. 8. I. Prickle of Rose-plant. II. Portion of the stem of the Hawthorn (*Cratægus*), showing modified branches as spines arising in the axils of leaves.

mentary shoots are borne. The thorns, once developed, will last as long as the plant itself, but the leaves in the axils of which they

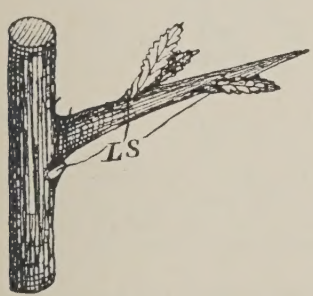


FIG. 9. A portion of the shoot of Sloe, showing a modified branch as a thorn. LS = leaf-scars of fallen leaves.

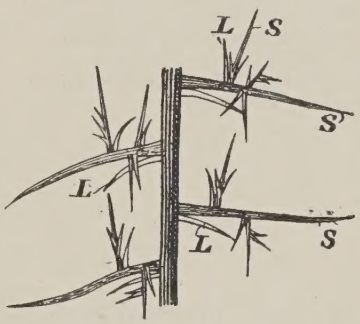


FIG. 10. A piece of the shoot of the Gorse, showing modified leaves and stems as spines. L = modified leaves; S = modified stems.

arose do not persist beyond the first year of their existence, though the leaf-scars (LS) may be seen for years subsequently.

In the gorse or furze both lateral branches and leaves are modified to form spines (Fig. 10, L & S). The leaf (L) is a lanceolate, pointed

spine, in the axil of which a very much longer, more or less, cylindrical spine arises, and which is therefore morphologically a modified branch; this bears other modified leaves and within their axils modified branches.

In the butcher's broom (*Ruscus aculeatus*, Fig. 11) the apparent leaves (S) are modified branches, as is shown by the fact that they arise in the axils of very small, scale-like leaves (L), and that they themselves often bear a similar leaf (L′) upon their upper surface.

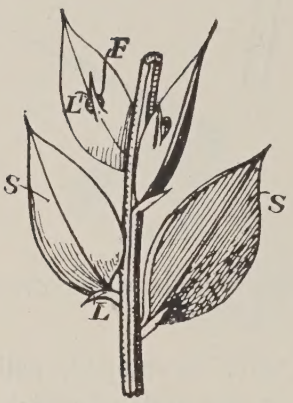


FIG. 11. A portion of the Butcher's Broom (*Ruscus aculeatus*), showing modified stems (S) as leaf-like organs. L = the true leaves reduced to scales; F = flower.

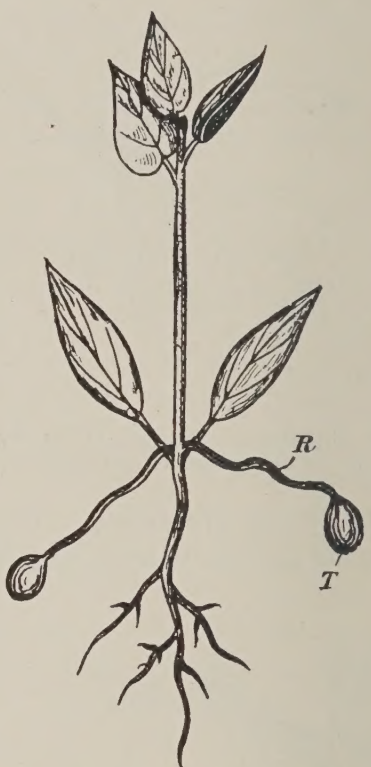


FIG. 12. A young Potato-plant, showing potatoes arising as swollen portions (T) at the end of underground stems or rhizomes (R).

Some of these modified branches also bear the flowers (F), which are small and lie in the axil of the leaf borne upon their upper surfaces.

Potatoes are modified stems, not roots, as popularly supposed. They are developed as swollen parts (Fig. 12, T) of underground portions (R) of the stem of the plant, in which food-material is stored up for the growth of the plant in the following year. If an old potato, one with its 'eyes' very apparent, be kept in a damp, warm place for a short time, the 'eyes' will develop into shoots, thus showing them

to be of the nature of buds, and from the base of the shoots roots will arise. The fact that the potato bears shoots demonstrates its stem

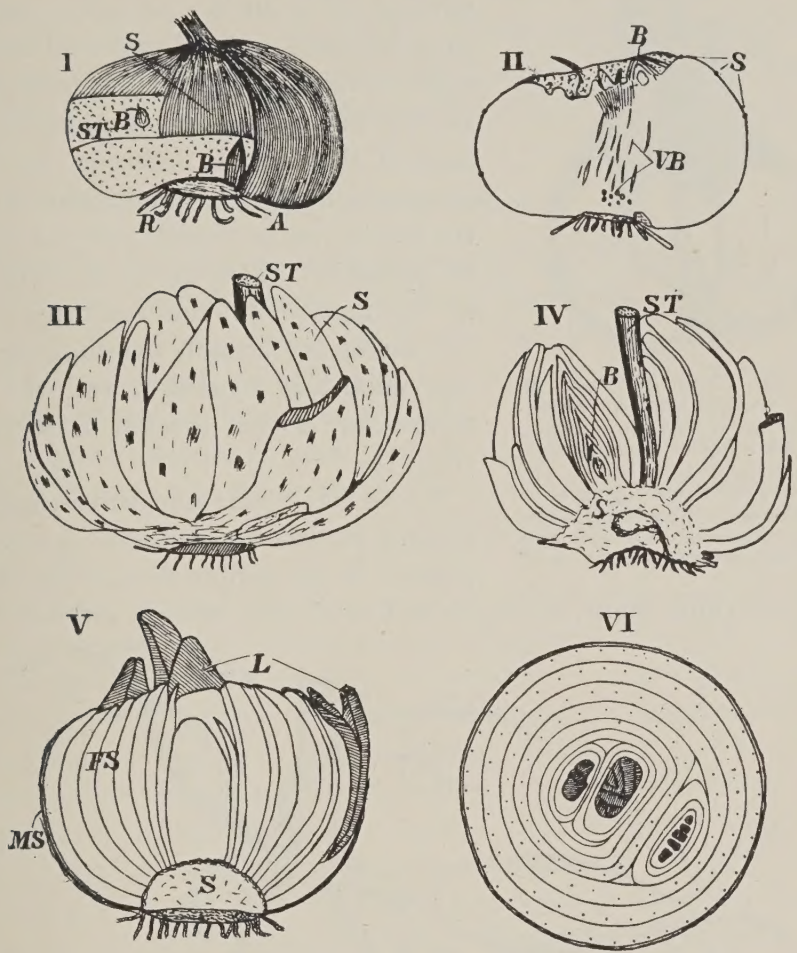


FIG. 13. I. Corm of Gladiolus. Portions of the membranous investing scales have been removed to show the thick stem. A = remains of last year's corm; B, B = accessory buds which may separate and form new plants; R = roots; S = covering scale-leaves; ST = red swollen stem. II. Median vertical section of the same. B = bud which develops into the current year's flowering shoot. The lower portion of the shoot formed from B forms the next corm; S = points of insertion of scales; VB = vascular bundles. III. Scaly bulb of the Lily. S = fleshy leaves; ST = old stem. IV. The same in median vertical section. B = bud which develops into the current year's aërial shoot; S = flattened stem with roots; ST = remains of last year's aërial stem. V. Median vertical section of tunicated bulb of Hyacinth. FS = fleshy leaves; L = green leaves; MS = thin dry outer scales. VI. Transverse section of tunicated bulb of Onion. The shaded structures in the centre are the shoots of the current year.

nature, for roots never develop shoots. Such swollen portions of underground stems are called **tubers**.

Bulbs and corms (Fig. 13) are modified plants, in which some organs are more modified than others. In corms, the base of the stem (ST) is abruptly round and swollen and contains stored up food-

material; it is invested in brown, scarious, scale-leaves, and the vegetative and floral shoots arise at various parts on it. In bulbs, the stem (S) is flattened and reduced, and the basal parts of the leaves become succulent and swollen and store up food-material. The form of the stem in bulbs is due to the suppression of the internodes, so that the leaves are as closely inserted together as possible. Two kinds of bulbs may be distinguished: the tunicated, where the leaves are broadly overlapping, as in the onion and hyacinth, and the scaly where they do not overlap, as in the lily (Fig. 13).

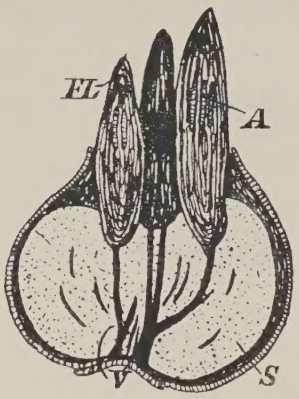


FIG. 14. Corm of Crocus in median vertical section. A=anthers of flower-bud; FL=foliage leaves of shoot of current year, not yet developed; S=stem. The black strands (V) passing through the stem are vascular bundles, and the thin membranous investments of the stem are scale-leaves.

Roots, like stems and leaves, may also become modified to subserve special purposes. In the garden dahlia (Fig. 14, TR) and in orchids, some of the older lateral roots become swollen during

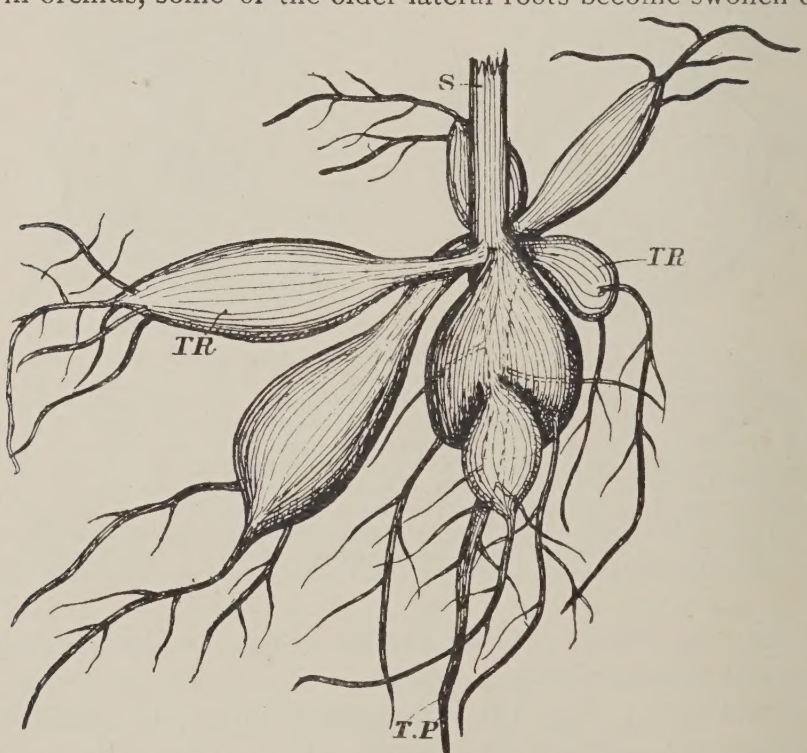


FIG. 15. Tuberous roots of the garden Dahlia. S=stem; T.P=lower part of the main root; TR=tuberous swellings of lateral roots.

the summer and autumn, and store up food-material for the growth of the plant of the following year; such roots are called **tuberous roots.** They can always be distinguished from tubers or underground stems by the fact that they never bear buds. In the carrot and beet, it is not the lateral roots, but the tap-root which becomes swollen and assumes a fusiform shape, and in the turnip it becomes spherical in form.

(B.) The Flower.

Neither the flower of the bean nor that of the sunflower is a typical one, since they are both adapted to special conditions. It will, therefore, be necessary to study some other flower first, and we may start with that of the buttercup, as being one that is easily obtained and which shows all the salient features of a flower.

The gross structure of most flowers may be best ascertained by means of median vertical sections, i. e. by a section taken through the flower in the middle plane. The section is best made by cutting through the flower from the stalk end. If the cut surface of such a flower be examined, it will be seen that at its extremity the flower-stalk enlarges to form a **receptacle** or **thalamus** (Fig. 178, I) for the attachment of the different parts of the flower. The summit of this receptacle, which occupies the centre of the flower, bears a number of small, green, elongated, roughly pear-shaped bodies (C), which at their free extremities are prolonged slightly into an awn-like point. Each of these little bodies is called a **carpel**; and a careful examination of any one of them will show that its swollen part is a little hollow box, containing within a small oval body, the **ovule**; this box-like portion is called the **ovary**, and the elongated free extremity, which is continued upward from it, is the **style**; the latter bears near its extremity a sticky surface, the **stigma**, which under the microscope is seen to be due to a number of glandular hairs that secrete a sticky fluid. Each carpel thus consists of an ovary, style, and stigma, and encloses the ovules. We shall see later that each carpel is a modified leaf.

Arising from the receptacle beneath the carpels are to be seen a large number of filamentous bodies called the **stamens** (S); each stamen consists of a **filament** bearing at its upper and free extremity a swollen portion, the **anther.** If the anthers be examined, it will be found that they are covered with a yellow powder, which has been liberated by their splitting; this powder is the **pollen**, and consists

of a number of minute grains, each of which is called a **pollen grain.** The pollen is the material that is concerned in bringing about the fertilization of the egg-cell within the ovule, and as a result of which, the ovule ripens into the **seed,** and the ovary into the **fruit.** There is apparently nothing very leaf-like in such structures as stamens, but if a cultivated geranium or rose be examined, many of the stamens will be found in their entirety to be leaves, while others will have a leafy filament bearing the unaborted anthers. Obviously, then, under certain conditions, the stamens may become leaves, for transitional stages between them and the leaf-like petals may be traced.

Inserted on the receptacle beneath the stamens is an envelope or **whorl** of five yellow, leaf-like structures, called the **petals**; each petal is independent of the other, but in many flowers the petals are fused together to form a more or less tubular investment. If we examine the upper surface of any of the petals, near its base, we shall find a small prominence, which is formed by a lid-like structure covering a small depression; this latter is the **nectary.** Nectaries are usually modified portions of some part of the flower, sometimes involving the petals, sometimes sepals, stamens, or receptacle.

Attached to the receptacle beneath the whorl of petals is another whorl, composed of five smaller, green, leaf-like **sepals,** which alternate in their insertion with the petals. Like the latter, the sepals are free from each other, but in many plants they are more or less united.

We thus see that a flower, such as the buttercup, is composed of four whorls of organs: an outermost one of five sepals; within this the whorl of five petals; within this the whorl of numerous stamens; and in the centre the whorl of carpels. The outer whorl of sepals is collectively spoken of as the **calyx**; that of the petals as the **corolla**; that of the stamens as the **androecium**; and that of the carpels as the **pistil** or **gynæcium.**

Of these four whorls, only the androecium and gynæcium are necessary for the performance of the functions of the flower, for the calyx and corolla, though advantageous as accessory organs, are not absolutely requisite for the production of seed. The two outer whorls serve in part to protect the two inner essential ones, and in part to attract insects by virtue of their colour, scent, and nectar. There are not a few flowers, those of many of our forest trees and of the nettle, in which the calyx or corolla, or both, are absent, and in some the androecium or gynæcium may also be absent. A flower, such as the buttercup, in which all four whorls are present, is called a **com-**

plete flower, and those in which one or both of the outer whorls may be absent, an **incomplete** one; but if both of the essential whorls are present, it is called a **perfect** flower, and **imperfect** if either of them be absent.

The androecium is the male portion of the flower, and the gynæcium or pistil, the female. Flowers which have both male and female organs present are called **hermaphrodite**, and those in which only one of these organs is present, **unisexual.**

The **bean-flower** is a complete one. The calyx is cup-shaped, and the five sepals of which it is composed are coherent, so that it forms a continuous investment round the basal portion of the flower; the dorsal margin (that directed downwards) is incised to form three prominent teeth, while the ventral margin is indented in the middle line; this indentation is the last indication of the fusion of the two adjoining sepals. The three teeth plus the indentation indicate that the calyx is composed of five sepals.

The corolla is much modified; it is composed of five petals, of which three are free and two are fused together. The upper petal is a broad expanded shield-like structure, slightly arched from side to side, and called the **standard** or **vexillum**; on either side within the standard is another petal, the **ala** or **wing**; and within the alæ, forming the lower boundary of the corolla, is a boat-shaped structure, the **keel** or **carina,** composed of two petals fused together along their inner margins.

The androecium (Fig. 154, V, S), like the corolla, is much modified. It is composed of ten stamens arising from the floral receptacle below the gynæcium and above the corolla; of these, nine are fused together along their filaments, the anthers and the terminal portions of the filaments remaining free, while the remaining one is independent and lies in the middle line below the standard. The cohering filaments of the nine stamens form a boat-like structure which lies within the carina; the upper open portion is closed by the filament of the free stamen, the form of which is adapted to the margins limiting the open part. In many plants of the pea and bean tribe (*Papilionaceæ*) (Fig. 154, IV) all ten stamens cohere together; the androecium is then said to be **monadelphous**, and when one remains free, as in the bean, it is **diadelphous.**

The gynæcium is composed of a single carpel, elongated in form, which lies within the fused filaments of the stamens. The style (ST) is very short and the stigma is merely the free extremity of it.

Within the ovary there are a number of ovules attached to the ventral margin. Each ovule is somewhat kidney-shaped in form, and is attached to the ovary wall by a very short stalk or **funicle**. With the aid of a simple lens, a very small aperture may be seen in the depression or hilum and situated very near to the funicle; this is the **micropyle**, present in all ovules, and through which the contents of the pollen grain pass to reach the egg-cell within.

Growing out as a ridge-like projection of the receptacle and encompassing the base of the ovary, is a fluted, yellow, corona-like structure, the nectary. It is situated between the base of the pistil and the cohering filaments of the androecium; and since the nectary forms the nectar, which is sought after by several species of insects, notably bees and wasps, the reason of the one free stamen is now intelligible. Were all the stamens united, as in some leguminous plants, they would form an investing tube round the ovary and nectary, and the proboscis of bees would not be able to reach the nectar; but by having one stamen free, the insect is enabled to force its proboscis through to the nectary, in the space which is left, when the free stamen is displaced. The bean-flower is one which depends upon the visits of insects for pollination and consequent formation of seeds, and one of the attractions which flowers offer to insects is the nectar which the nectaries secrete. Hence, in the bean-flower we find the stamens so adjusted as to render the nectar accessible to insects, for were it otherwise, the bean-plant would become eliminated as a race through the failure of insects to visit it, with the consequent non-pollination of the flower and nonformation of its propagating seeds.

The flower of the **sunflower** is not a single one, but an aggregate of many inserted on a much enlarged disc-like receptacle (Fig. 16, R), which is hidden by a covering of bracts (B). The flowers are of two kinds: the **ray florets**, which are arranged round the circumference of the receptacle, and possess large, yellow, strap-shaped corollæ (CR); and **disc florets**, which occupy the remaining portion of the receptacle, and have smaller and tubular corollæ terminated by five teeth.

When bracts are arranged in a whorl or series of whorls, and surround or are in relation to an aggregate of flowers, they are said to form an **involucre of bracts**; and inserted upon the margin of the receptacle (Fig. 16, B) there is such an involucre composed of several whorls of green, pointed bracts, of which those of the outer whorl are larger than those of the inner ones. In addition to these bracts, there are others (B′) situated upon the upper surface of the

receptacle, each of which is related to a particular floret; these are called **bracteoles**, and they are somewhat membranous in texture and forked at their apices, each prong being acutely pointed and one longer than the other. In the axil of each of these bracteoles, a floret arises.

The gross structure of a flower-head of the sunflower is best studied by cutting it in half in a median, vertical plane. The cut surface of such a preparation is represented in Fig. 16, where the involucre of bracts (B) can be seen arising from the circumference of the receptacle (R), and inserted upon its surface are the florets. Each floret is supplied by a small branch derived from the vascular bundles (V. B) of the stem. The florets are of two kinds and of different

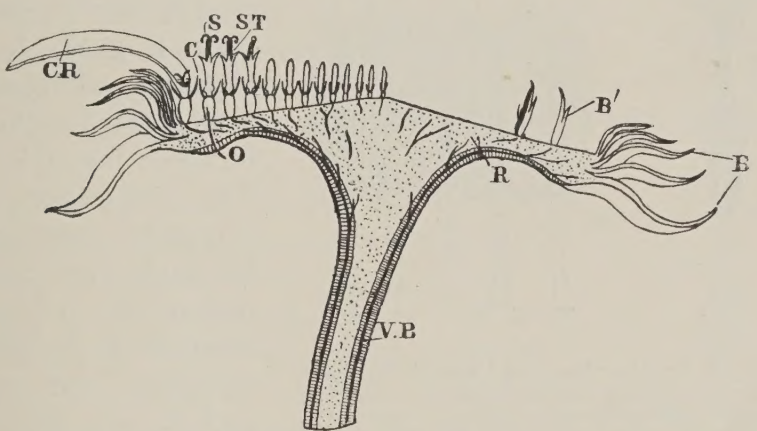


FIG. 16. View of the cut surface of a bisected Sunflower. B = involucre of bracts. B' = bracts, in the axils of which the florets arise; C = calyx; CR = corolla of a ray-floret; O = ovary; R = receptacle; S = stigma; ST = stamens; V B = vascular bundle.

ages: those in the centre of the receptacle are the youngest, those on the periphery the oldest, so that as we proceed from the periphery to the centre we pass through successively younger florets.

Examination of a disc floret shows that the **ovary** (Fig. 17) is composed of a single compartment, with a single ovule (OV) attached to its floor, and that it is situated beneath all the other parts of the floret; from the central portion of the upper part of the ovary the elongated **style** arises, and which terminates at its other end in the bifid (or forked) and recurved **stigma** (S). From the circumference of the upper portion of the ovary, the tubular, five-toothed corolla (CR) has its origin; at its base it is contracted, then forms a bulbil-like enlargement and above this is uniformly tubular. The enlargement is due to a band-like thickening of the corolla wall, which

forms the **nectary** (N). The corolla thus differs from that of the bean-plant or the buttercup, in that the five petals (indicated by the number of teeth) are confluent and form a tubular investment, and arise from the summit of the ovary and not beneath it from the flower stalk.

The androecium is peculiarly modified. The filaments of the stamens (ST) are attached at their basal ends to the basal portion of the corolla, upon its inner surface, and just along the lower margin of the ring-like nectary, but the anthers closely invest the upper portion of the style and, in the younger florets, the stigma also, the lateral margins of each anther being connected with those on either side of it by delicate strands of tissue (Fig. 17, II, P); the coalesced anthers thus form a tube, through the lumen of which the style passes. The androecium of the sunflower therefore exhibits the converse condition of that of the bean-plant flower, in which the filaments and not the anthers are united; the androecium of the sunflower is said to be **syngenesious**, on account of the union of the anthers, and it is a character diagnostic of the natural order, *Compositæ*, to which the sunflower belongs. The stamens can be best studied by detaching a single, tubular (disc) floret, slitting open the corolla along its length by means of a needle, detaching the filaments from their connexion to the petals, slitting open the ring of anthers, and removing the whole to a slide, mounting in water, and examining with a very low power of the microscope. The five anthers can then be seen to be united to each other by their margins, and each to consist of two **pollen-sacs** (Fig. 17, P.S) or elongated cavities containing the **pollen**, and connected to each other by a central strand or column of tissue, the **connective** (CN), continuous with the **filament** (F) below and with a leaf-like appendage (A) above.

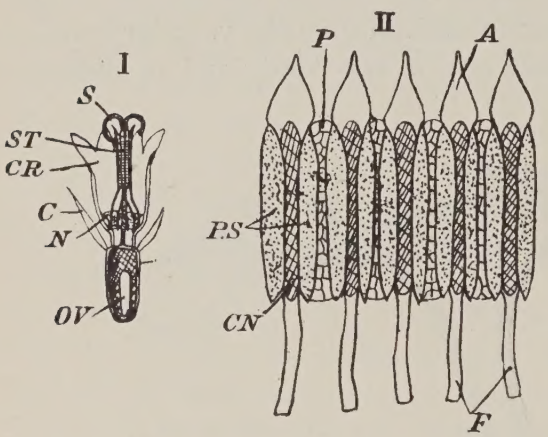


FIG. 17. I. Interior view of a bisected disc-floret of the Sunflower (*Helianthus annuus*). II. The syngenesious androecium split open with a needle and laid out flat, and examined under a low power of the microscope. A = leaf-like appendage of stamen; C = calyx; CN = connective; CR = corolla; F = filament; N = nectary; OV = ovule situated in the ovary; P = thin parenchymatous tissue forming the connective; P.S = pollen-sacs; S = stigma; ST = stamens.

The **calyx** (C) is reduced to two membranous, scale-like sepals. In some *Compositæ* the calyx is absent, and in others, such as the dandelion (Fig. 18, C), it consists of a whorl of feathery filaments, called a **pappus.**

The structure of the ray floret is different. The relative arrangement of calyx, corolla, and ovary is the same; but the corolla (Fig. 16, CR) is not tubular, except for a very short distance from its base, but is flattened to form a broad, showy, yellow leaf-like structure. On account of its strap-shaped form it is called a **ligulate corolla.** It is the expanded petals of the ray florets that form the showy marginal expanse of the flower. The androecium is aborted and stamens are, therefore, absent. On some few of the ray florets a reduced stigma and style may be found, but in the majority they are not present; all of the ray florets possess an ovary, but there is no ovule within them.

FIG. 18. The fruit of the Dandelion (*Taraxacum officinale*), to show the nature of the feathery calyx (C). The oval body at the bottom, and from which the calyx arises, is the ovary.

The ray florets thus contain none of the essential portions of the sexual apparatus and in consequence are said to be **neuter.** They serve, in virtue of their showy corollæ, to attract insects. In many *Compositæ* the ray florets may contain a functional style, stigma, and ovule, or functional stamens, but not both; such florets are said to be **unisexual.** In other *Compositæ* all the florets are hermaphrodite, or all male or female. Such flower-heads are said to be **homogamous** in distinction to those, called **heterogamous,** which contain, like the sunflower, two sorts of florets. Another example of a heterogamous flower-head is that of the daisy, where the disc florets are hermaphrodite, and the ray florets unisexual. The dandelion (*Taraxacum officinale*) has a homogamous flower-head, all the florets being ligulate and hermaphrodite (bisexual); its receptacle, unlike that of the sunflower, does not bear bracteoles, and is said to be **naked,** to distinguish it from the **palæaceous** receptacles which do.

2. Internal Structure.

(A.) The Vegetable Cell and its Chief Modifications.

Before approaching the study of the minute structure of the stem of the sunflower or bean-plant, it is necessary that the student should have some elementary knowledge of the general properties of the plant-cell, and of the changes in form, and chemical and physical nature which it may undergo.

If a small portion of the pulp of an apple be well teased, by means of two needles, in a drop of water on a microscope slide, so that it is broken up into the smallest possible fragments, and then examined beneath the low and high powers of the microscope, it will be seen that the pulp is composed of minute, colourless, more or less regularly oval or polygonal sacs. Some of these will still be associated in groups and others will be isolated. Examination of a single **cell** or **sac** shows that the **cell-wall** (Fig. 19, I, CW) is composed of a delicate membrane which encloses a film of granular material, the **protoplasm** (P), constituting a kind of jelly-like covering to its internal surface. The central portion of the cell, bounded by the protoplasm, is occupied by a watery fluid, the **cell-sap**; the space filled with the cell-sap is called the **vacuole** (V), or cell-cavity. By means of various staining substances, of which methyl green acidulated with two per cent. acetic acid is the best, a small oval body, the **nucleus**, may be seen embedded in some portion of the protoplasm. The advantage of employing methyl green is that it stains the nucleus alone, and leaves the protoplasm and cell-wall unstained. The protoplasm is the living portion of the cell, and is the stuff that is universally associated with life; it is fundamentally of the same nature in both animals and plants, and chemically it is composed of a mixture of nitrogen containing bodies of a highly complex and unstable molecular constitution, called **proteids**, which contain the four elements **carbon**, **hydrogen**, **nitrogen**, and **oxygen**.

The vegetable cell differs from the animal cell in the possession of a definite cell-wall. The nature of this cell-wall, therefore, becomes a matter of importance, especially since, with but one or two doubtful exceptions, all plant-cells, at one period or another of their existence, possess it.

Until recently it was thought that, chemically considered, the unaltered cell-wall was wholly composed of a substance which has the same

formula as starch, but very different chemical and physical properties It has received the name of **cellulose** and can be identified by several definite reactions. When treated with a compound of chlorine, zinc, and iodine, known as chlor-zinc-iodine or **Schultze's solution**, it gives a blue or sometimes a purplish-blue colouration ; or, if treated first with 50 per cent. sulphuric acid and then with iodine solution, it also gives a blue colouration. Recent investigations, however, have shown that the cell-membrane is not wholly composed of cellulose, but of this closely associated with other bodies. If the membrane be treated with an ammonio-cupric sulphate solution (Schweizer's reagent) the cellulose is extracted from the cell-wall, which, however, still retains its form unaltered, thus showing that some other substance or substances are present. These are known as **pectic bodies**, and they may be arranged in two series, one of which contains neutral substances and the other feebly acid ones. Each series contains several bodies, but the two important ones in the former series are **pectose** and **pectine**, and in the latter **pectic** and **metapectic acids**. Of these four substances, pectose and pectic acid (the latter usually in combination with calcium, as calcium pectate) are the most frequently occurring. In young cells, such as those found in the apical meristem (cp. p. 72), pectose appears to be the body associated with the cellulose, the calcium pectate being present in only small proportions ; but in older cells the proportion of calcium pectate is much larger. In both old and young cells the middle lamella (Fig. 19, ML, cp. p. 47) is composed exclusively of calcium pectate. The manner in which the cellulose and pectic bodies are associated is not yet certainly determined, but it must be a very intimate one, and probably also only a mechanical one, since the two bodies can be separated. Pectine is a body soluble in water, in the process of which it swells and gelatinizes ; it is readily extracted from ripe fruits, such as apples, and it exists in many mucilages. Pectic acid is insoluble in water, alcohol, and acids ; it forms soluble pectates when treated with alkalies, and insoluble ones with the alkaline earths. Dissolved in alkaline carbonates it forms a mucilaginous solution, but dissolved in oxalate of ammonia it forms a perfectly fluid one.

Another instance of a living cell may be seen in the hairs on the stamens of *Tradescantia*. If a few of these be examined in water, under the microscope, it will be observed that each hair is composed of a few cells arranged in linear series, and that each cell has the same structure as those of the apple pulp, though the nucleus will be difficult

to see on account of the purple colour of the cell-sap. But the protoplasm is not quiescent; it is slowly and continually circulating, moving currents passing backwards and forwards in all directions,

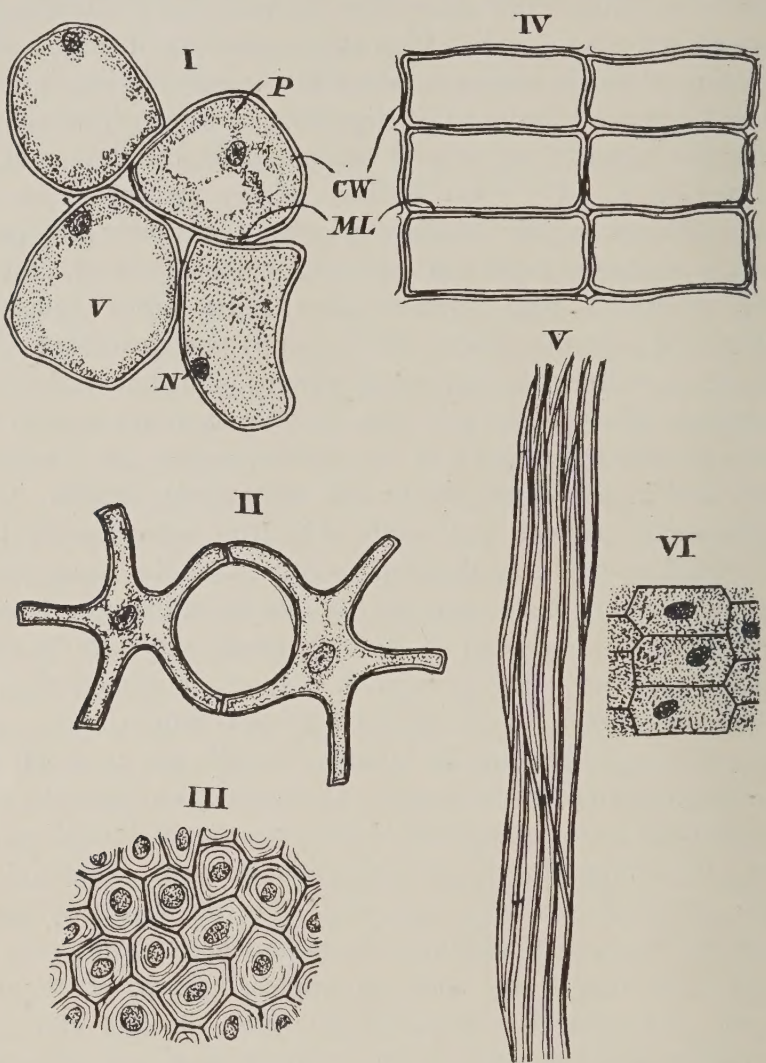


FIG. 19. I. A few cells from the pulp of the Apple, teased out with needles and examined under a one-sixth objective of the microscope. II. Stellate cells from the stem of the Rush. III. Thick-walled cells from the endosperm (so-called 'stone') of the Date-palm. IV. Cork-cells. V. Prosenchyma fibres. VI. Young cells from seeds of the Apple. CW = cell-wall; ML = middle lamella; N = nucleus; P = protoplasm; V = vacuole.

and all trending to or from the centrally situated nucleus. This movement of the living protoplasm is not an uncommon phenomenon, and may be seen in many plant-cells.

The staminal hairs of *Tradescantia* afford very good opportunities

for studying a very important property of living cells: that of **cell division.** If a stamen with its hairs be removed from a flower-bud on a warm day, and placed in a 1 per cent. solution of sugar, and one of the terminal cells of the hairs be examined, from time to time, beneath the high power of the microscope, it will be seen to undergo the process of dividing into two. The nucleus gradually elongates in the direction of the long axis of the cell; then it presents a striated appearance, the fibrillæ meeting each other at either pole of the nucleus; the fibrillæ are then ruptured across the equatorial plane and either portion aggregates at the nuclear poles, so that two new nuclei are formed; a layer of granular protoplasm now forms itself in the equator of the cell and between the two new nuclei; this layer becomes converted into cellulose and thus forms a new cell-wall, dividing the original cell into two cells, each with its own nucleus. This process may be repeated, once and perhaps twice, but in these particular cells it is not indefinitely repeated. We thus learn that, previous to the division of a cell, its nucleus first divides; the division of the nucleus being preceded by the appearance of fibrillæ definitely arranged. The fibrillæ are really minute threads, derived by the splitting into a definite number of parts of a nuclear skein.

If one of the leaves of any moss (Fig. 20, I) be removed and examined in water, beneath the microscope, it will be seen that it is composed of a number of cells, oblong in form, arranged to form a lamina, a single layer only of cells in thickness. Careful examination of any one of these cells will show that it is fundamentally the same as any of those from the apple pulp or the staminal hairs of *Tradescantia*: that is, it consists of a cellulose cell-wall (CW), protoplasm (P), nucleus (N), and cell-sap. But in addition there will be seen certain **cell-contents**, in the form of round or oval, green grains, called **chlorophyll grains** (CG), **plastids**, or **corpuscles.** The green colour of all green plants is due to the presence of chlorophyll corpuscles embedded in the cell protoplasm. If the moss leaf be immersed in alcohol for a short time, the green colouring matter will be extracted by solution in the alcohol. If such a decolourized leaf be examined under the microscope, the green grains will no longer be seen, but in their place a number of colourless grains of the same form, size, &c. as the chlorophyll corpuscles. Obviously the chlorophyll granule consists of two portions: a colourless grain, and a green colouring solution which can be extracted from it by means of alcohol. The colouring matter is called **chlorophyll**, and the grain

within which it is contained, a **plastid.** The latter are differentiated, denser portions of the protoplasm. And if they be treated with picric acid and then with alcohol, and subsequently stained with hæmatoxylin, and examined beneath high powers of the microscope, they will be seen to have a trabecular or spongy structure. We may, therefore, infer that the chlorophyll is lodged within the meshes of the plastid.

If the leaf has been exposed to sun-light for some time before bleaching by alcohol, the plastids will show embedded in their

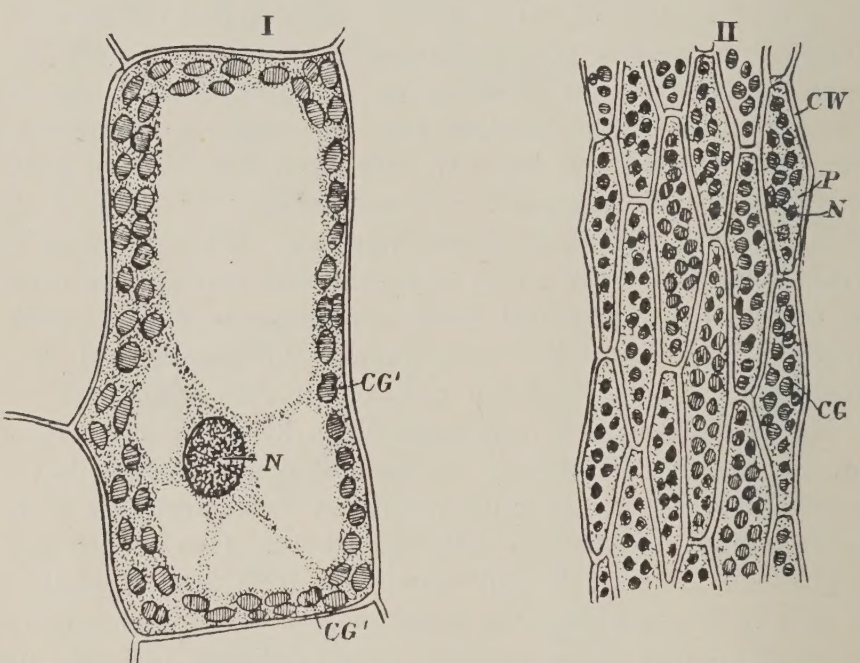


FIG. 20. I. A single cell of a moss leaf examined under the one sixth objective and magnified about 350 times. II. A portion of the leaf of the Canadian Water-Weed (*Elodea Canadensis*) examined in water under the two-thirds objective and magnified about 75 times. It is seen to be composed of elongated cells. CG = chlorophyll grains; CG' = chlorophyll grains dividing; CW = cell-wall; N = nucleus; P = protoplasm.

substance a number of bright, refractive dots or granules. If the plastid be stained with iodine, or better, treated for some hours with a solution of iodine in chloral hydrate, these granules will stain dark blue; this reaction, taken in conjunction with others, shows them to be **starch granules.** Starch is a food-material which the plant utilizes as occasion demands, and we see that it is formed within the chlorophyll plastids.

Careful examination of the chlorophyll plastids in a living leaf will show that they multiply in number by the process of division (Fig. 20,

II, CG'). Each grain divides into two, which grow to the size of the parent grain ; each grain may then divide again and grow.

All that has been described as existing and occurring in the cells of the moss leaf may be equally well seen (Fig. 20, II) in those of the leaf of the Canadian water-weed (*Elodea canadensis*). But in addition, the chlorophyll granules will be observed to slowly travel round and round the cell, carried by the moving protoplasm. The movement of the protoplasm here differs from those in the cells of the staminal hairs of *Tradescantia*, in that it is one of **rotation** and not of **circulation.**

We have seen above, that starch is formed in the chlorophyll corpuscles ; this is true, in the long run, of all starch. But starch may be secondarily formed in parts of plants in which no chlorophyll occurs, as in the tubers of the potato, orchids, &c. But the starch is formed differently and from different material in the two instances: that formed in the chlorophyll is the direct product of assimilation—is the product of those physical and chemical changes by which the CO_2 of the atmosphere and the H_2O of the soil are decomposed and reconstituted into starch—while that formed apart from chlorophyll is the product of dehydrated sugar, which is derived from the starch formed in the chlorophyll (see chap. XXIII, pp. 412, 442).

The conversion of the sugar into starch is brought about by the agency of differentiated portions of the protoplasm of the cell, similar in nature, though different in their activities, to the chloroplastids (chlorophyll plastids), and since they are starch-forming bodies, they are called **leucoplastids** (Fig. 213). If the freshly cut surface of a potato be scraped and the matter mounted in a little water and examined under the microscope, there will be seen a large number of oval, colourless, highly refractive bodies : these are the **starch grains.** At one end of each of these grains there is a bright dot, the **hilum** (Fig. 211), around which concentric striæ are arranged ; the hilum is the oldest—first formed—portion of the grain, and the striæ represent layers of different density, some layers containing more or less water than others. Treated with a weak solution of iodine, the grains stain blue, more or less dark, according to the strength of the solution : this is the characteristic reaction of starch. Treated with a solution of caustic potash or chloral hydrate, or heated to a temperature of 65° C., they swell and lose their high refractive index (become duller in appearance), though they still retain their characteristic reaction with iodine.

If instead of scraping the surface of a potato, we examine thin sections of one, taken just beneath the corky rind, or sections through the tubers of an orchid (*Phagus*), or the rhizome of *Iris* or *Canna*, we shall find that the starch grains are attached to other grains, the leucoplastids (Fig. 213). In some of these the starch grains will be larger than the plastids, in others the plastids are larger than the starch grains, and in others intermediate stages may be seen. In some the starch grains will be very large, and the plastid a mere speck; in others no plastid will be seen. Obviously, as the starch grain increases, the plastid decreases; the one grows at the expense of the other. The plastid is the living grain; the starch is the organic but inanimate product of its activity. Stained with iodine solution the starch is coloured blue, and the plastid brown or yellow-brown. The forms of the plastids vary with different plants: in the potato they are spherical or oval, and in the orchid rod-like. As a rule, but one starch grain is formed in each plastid, but sometimes two grains are formed, and continue to grow until they meet; in this way **compound starch grains** are formed.

In addition to leucoplastids and chloroplastids, other plastids of essentially the same nature, but differing in form and tint, are to be found in many fruits and coloured petals. In the cells which constitute the pulp of the tomato and other fruits, there are to be seen coloured granules of more or less regular form; these are the **chromoplastids**, and to their presence the colour of the fruit is due. Similar bodies may be seen in the petals of the nasturtium, and in the staminal hairs of the vegetable marrow. The colour of other petals, e. g. geranium, and of the root of the beet, is due, not to chromoplastids, but to a coloured cell-sap.

Oil, in the form of **oil-drops**, is a very frequent constituent of cell-contents in seeds and fungi. In some measure it takes the place of starch as a reserve food-material, and in other instances gives rise to starch by processes which we shall study later. Examination of thin sections through the cotyledons (seedling leaves) of the almond seed will reveal the presence of a number of bright-looking (highly refractive) dots in the cells; if treated with ether the substance of the dots is dissolved; if stained with tincture of alkanet they assume a pink colour; if with osmic acid, a black or dusky hue; treated with potash and warmed, they assume at first a milky appearance (due to saponification), and finally dissolve. These are characteristic reactions for fat.

Aleurone grains (Fig. 215) are proteid granules, the precise nature of which varies slightly in different plants. They may most readily be seen in the endosperm of the seeds of the castor-oil plant, by making a transverse section and mounting in either olive or castor oil. Each grain is somewhat oval in form, and has a high refractive index, as is evidenced by its bright appearance; at one end a dark round body, the **globoid**, may be seen, and which is chemically a phosphate of calcium and magnesium. Examined in water, the aleurone grain swells and becomes less highly refractive, and within it there will then be seen, in addition to the globoid, certain hexagonal bodies, one or two in number, called **crystalloids**; they are so called because they possess a crystalline form, but they do not otherwise possess any of the characters of crystals; in chemical composition

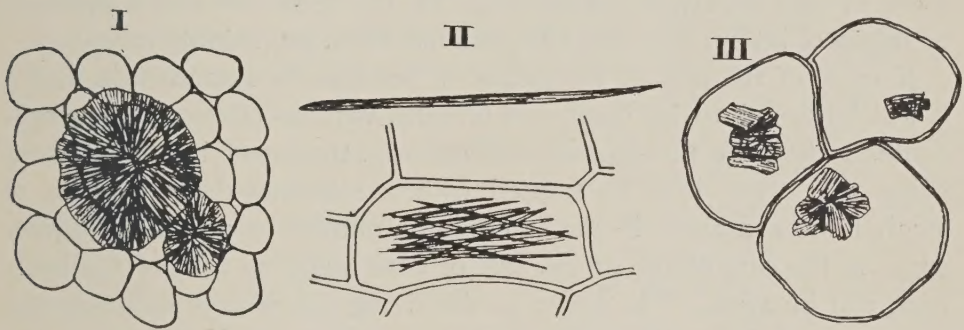


FIG. 21. I. Section through the soft tissue (parenchyma) of the Jerusalem Artichoke, showing the sphere-crystals of inulin with a radiate structure. II. The lower figure shows a single cell from the leaf of the Hyacinth, containing raphides. The upper figure shows a single raphide. III. A few cells from the petiole of a Begonia, showing crystals of calcium oxalate.

they are, like the aleurone grains within which they lie, proteid in nature.

Crystalloids, apart from aleurone grains, may be seen in the superficial cells of the potato tuber. They are cubical in form, and, like those of the castor-oil seed, are soluble in potash and salt solution.

Crystals, mainly of calcium oxalate and calcium carbonate, are to be found in the tissues of a large number of plants. Sections through the petiole of a begonia (Fig. 21, III) will show the presence of somewhat star-shaped crystalline bodies, which are really compound crystals, that have formed together in a complex manner; treated with acetic acid they do not dissolve, so they are not, therefore, calcium carbonate; treated with dilute nitric acid they readily dissolve; these facts, coupled with what is known as to the composition of the ash of the petiole, lead us to infer that they are crystals of

calcium oxalate. In many of the cells in the leaf of the hyacinth or onion, bundles of needle-like crystals, called **raphides** (Fig. 21, II), are to be seen ; they react in the same way towards reagents as those in the petiole of a begonia, and are therefore probably composed of calcium oxalate.

The cells of certain parts of plants very often contain reserve food materials in a state of solution. A section through the tuber of the Jerusalem artichoke, if examined in water, will show ordinary thin-walled cells ; but if they be examined in alcohol a granular precipitate of **inulin** will be seen within them. If portions of the tuber are preserved in alcohol for some months, sections then cut from it and examined in alcohol will show the inulin deposited in the form of needle-like crystals, radiating from a common centre and forming more or less spherical masses (Fig. 21, I) ; these are called **sphere-crystals** of inulin, and, like the granular form, are soluble in water.

If some of the pulp of the grape or beetroot be examined in water, it will be found to be composed of cells, with no other apparent cell-contents than the protoplasm and cell-sap, the latter in the beetroot being red. But if it be treated with a relatively large volume of alcohol and examined in that medium, a number of crystals of grape-sugar in the case of the grape, and of cane-sugar in that of the beet-root, will be seen. The sugar in the living cell is in solution in the cell-sap, but being insoluble in alcohol is precipitated upon the addition of that reagent.

We have thus far learned that an unmodified cell is of the nature of a sac, the wall of which is composed of cellulose, and which encloses the living protoplasm with its embedded nucleus as well as the cell-sap. The protoplasm may also enclose various bodies, which may be grouped together as **cell-contents.**

All plants, however complex their ultimate organization, arise from a single cell of fundamentally the same kind as any of those from the apple pulp, or any one of those forming the staminal hairs of *Tradescantia.* But an examination of the tissues of which the stem, leaf, or root of any of the higher plants, such as the sunflower or bean-plant, is composed, shows that many kinds of cells, some of them very much modified, are present. Having thus studied the primitive structure of a cell, we must next proceed to study the modifications which such a cell can undergo in order to give rise to the constituent elements of diverse tissues.

Broadly speaking, a cell may undergo two kinds of changes : that

of form, and that of a chemical and physical alteration of its protoplasm and cell-wall.

Changes resulting from an alteration of form give rise to two classes of tissues: **parenchyma** (Fig. 19, I, IV, V), in which the cells are applied face to face and are not much longer in one direction than another; **prosenchyma** (V), in which the cells are much elongated in one direction, and are applied to each other by their tapering extremities.

Parenchyma is a tissue composed of cells, the walls of which are as a rule thin and of cellulose, and the cells are approximately square or oblong in form, though they may assume various other forms, such as the stellate (Fig. 19, II); they nearly always contain living contents, and are often crowded with starch granules or other reserve food-material, and also chlorophyll granules. Sometimes the cellulose cell-wall becomes very much thickened without undergoing any other change, as in the endosperm of the date seed (Fig. 19, III); but more usually when the wall becomes thickened, the cellulose undergoes a chemical and physical change and becomes converted, almost wholly, into a woody substance, **lignine**. Or it may become converted into a corky substance, impervious to gases or water-vapour, called **suber**; of such modified cells is cork composed; but in this instance the protoplasm of the cell becomes used up, and the cells are dead cells (Fig. 19, IV). More rarely the cellulose cell-wall becomes converted into a slimy material, called **mucilage**; linseed is an instance of this, for the sliminess produced when it is soaked in water is the result of the imbibition of water and consequent swelling of the mucilaginous walls of the cells which form the outer coat of the seed. In other cases, where the cells form an external layer, the cell-wall may, in part, become converted into a substance impervious to gases or water-vapour, called **cutin**.

All these substances can be identified under the microscope by appropriate reagents, of which the most generally useful is **Schultze's solution**. For the reactions of lignine, sections cut from any piece of wood will do. If such sections be treated with chlor-zinc-iodine (Schultze's solution) and examined beneath the microscope, the cell-walls will stain yellow. Treatment with iodine solution produces the same reaction. Treated with a weak acid solution of **aniline sulphate**, the walls stain a bright, chrome yellow. These reactions serve at once to distinguish lignine from cellulose, which with Schultze's solution is coloured blue or purple; with iodine only faintly yellow; and with aniline sulphate no result. Moreover, lignine does

not give the blue colouration when treated with iodine and sulphuric acid.

Suber or cork gives very similar reactions to those of lignine with iodine and Schultze's solution, but aniline sulphate does not affect it. Although lignine does not give the blue colouration with iodine and sulphuric acid, yet, like cellulose, it swells when thus treated; suber is like lignine in that it gives no colouration with this reagent, but it differs from it, in that it does not swell and the cell-walls retain their sharp outline.

Mucilage may be identified by the avidity with which it takes up water and swells; it swells more rapidly if treated with caustic potash. With iodine it does not stain, and with iodine and sulphuric acid only a very indistinct bluish tinge may be seen. It stains pink when treated with **corallin-soda** solution.

With some of the permanent and basic stains like **hæmatoxylin**, cellulose and mucilage stain intensely, while cork and wood (lignine) do not stain at all.

Prosenchyma (Fig. 19, V) is composed of elongated, pointed, fibrous cells, the walls of which are usually thickened and lignified; when the cells are lignified the tissue is usually called **sclerenchyma**, and in such cells the protoplasmic contents are much reduced or absent. When such cells occur in connexion with the vascular strands, they are called **xylem** or **wood fibres**.

Sclerenchyma fibres or **xylem fibres** are essentially supporting structures, and hence we find that their walls are very thick; in fact, many sclerenchyma fibres are so much thickened, that the original cell cavity becomes quite obliterated. In transverse sections, the thickened wall (Fig. 19, III) shows a stratified appearance, indicating that it has been formed by the addition of successive layers, superposed upon those previously existing. But this formation of successive layers is not deposited uniformly, for minute spaces are left where no secondary material is deposited; and every layer that is laid down leaves a little space in just the same place that its predecessor did, and that its successor will, so that little tubular canals are left, which pierce the whole thickness of the wall, with the exception of the outer primitive cellulose cell-wall. These little canals are called **simple pits**, and fibres which contain them are called **pitted fibres** (Figs. 23 and 24).

Vessels. Vessels are tubes that occur in connexion with the vascular strands, and are formed by the elongation of cells and

the absorption of their transverse walls (Fig. 22). Cells which are destined to give rise to vessels are arranged one above the other in serial order and are applied end to end. The end walls becoming absorbed, the cavities of contiguous cells thus become placed in communication, and if this occurs along a great length of cells, the result is the formation of a tube-like structure. In the case of vessels occurring in the wood, the longitudinal walls thicken in various ways, coincident with the absorption of the end walls. Perhaps one of the simplest methods of thickening of the wood vessels is that of the deposition of rings or hoops of wood (Fig. 23, I) on the internal surface of the primary cellulose wall of the vessel; the layer of woody material (lignine), instead of being deposited uniformly upon the primary wall, is laid down as a number of hoops, usually close together, but sometimes widely distant; such vessels are called **annular vessels**. A slight variation from this mode of thickening (Fig. 23, II) is the deposition of the lignine in the form of a spiral band upon the internal surface of the vessel, and which may assume a close or a very open form of spiral; these vessels are called **spiral vessels**. **Scalariform vessels** (Fig. 23, III), or vessels with ladder-like markings, are formed when the secondary thickening leaves a number of slit-like pits arranged one above the other, like the rungs in a ladder. **Reticulate vessels** are formed when the secondary thickening is laid down somewhat irregularly, so that the marking upon the wall is more or less mesh-like in nature. **Bordered-pitted vessels** (Fig. 23, IV, and Fig. 91, BP) are those in which the pit is not a simple canal or a slit-like cavity, but is concave in form, with the apex of the concavity opening into the lumen of the vessel and its base situated upon the

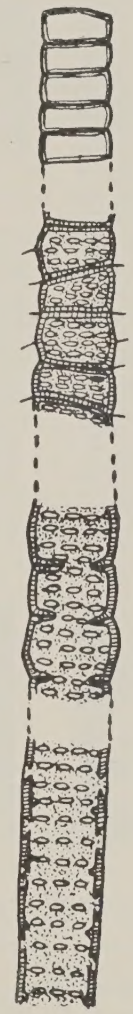


FIG. 22. Portions taken at different levels of a strand of cells, showing the mode of formation of a vessel by the absorption of the transverse walls of superposed cells, and the thickening and lignification of the others. The top portion represents the unmodified cells at the apex of a stem; the portion next below shows the thickening and pitting of the cell-walls; and in the part next below the transverse walls are partially absorbed. In the lowest part the transverse walls are wholly absorbed, so that the cavities of the cells are in communication, and the formation of the vessel is completed.

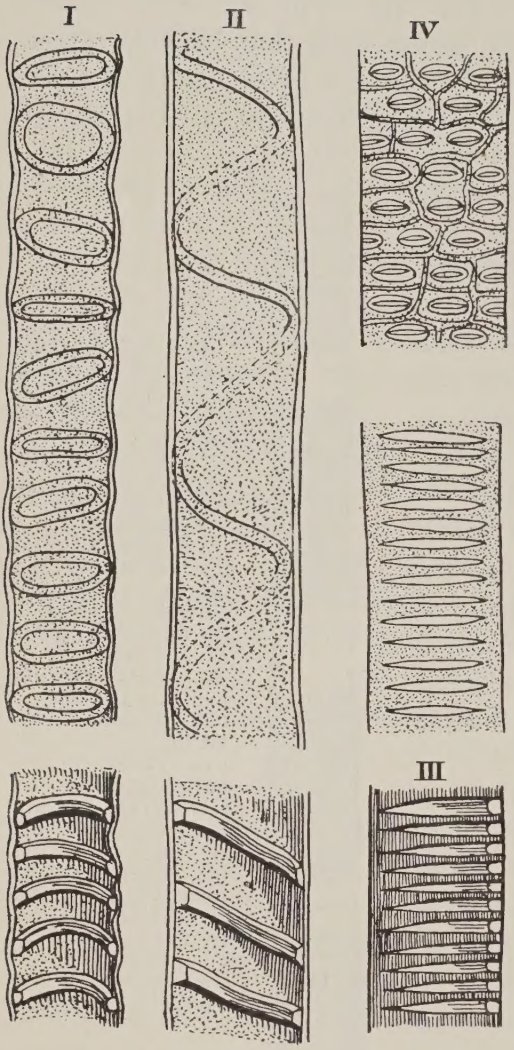


FIG. 23. Different kinds of vessels. I. The upper figure represents an annular vessel, with the annular thickenings seen through the thin wall; the lower figure represents the vessel bisected along its length and showing the rings as thickened hoops. II. A spiral vessel; the upper and lower figure respectively represent the same view as in I. III. A scalariform pitted vessel. The upper figure shows the vessel in surface view, and the lower an internal view such as may be obtained by median bisection of the vessel. IV. A reticulate and bordered-pitted vessel in surface view.

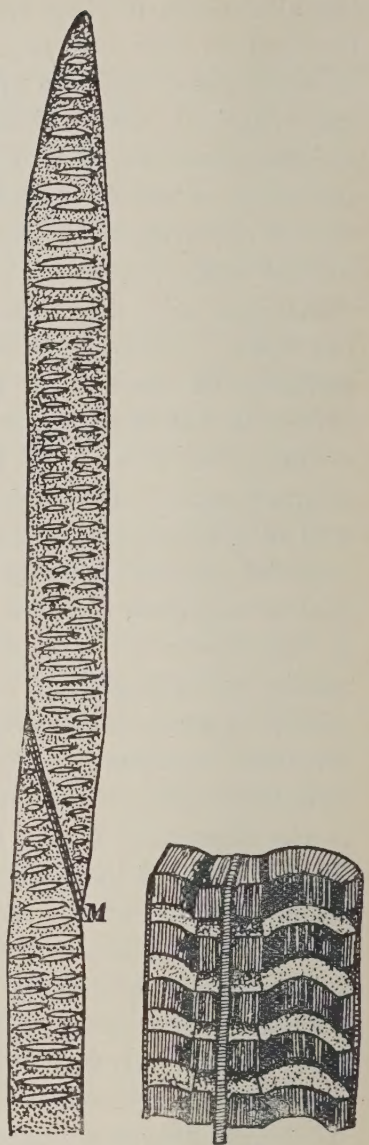


FIG. 24. Tracheid from the xylem of the Bracken Fern (*Pteris aquilina*). The left-hand figure shows the surface view, and the persistent transverse wall (M) of two contiguous tracheides. The pits are slit-like and arranged in a scalariform (ladder-like) manner. The right-hand figure represents a part of two contiguous tracheides highly magnified (about 300 times), from an internal view, showing the pits.

primary cell-wall. Such a pit looked at in surface view would show two rings: a central, smaller one corresponding to the aperture, and a larger one surrounding this, corresponding to the basal circumference of the pit. The pits in the walls of contiguous vessels are always opposite one another, so that in section the cavity of the pit is biconcave in form, and is traversed through its widest portion by the confluent primary membrane of the two vessels. In the centre of the pit this membrane is thickened to form a small pad-like thickening, called the **torus**. Bordered pits are formed by the successive layers of the lignine that are deposited during the thickening of the vessel, leaving a narrower space than the one that preceded it. The form of two contiguous pits may be readily conceived if the student will take two watch-glasses, which are flattened at their summits, and place them base to base with a piece of paper between. The paper will represent the primary wall upon which the torus arises as a thickening in its centre; the cavity between the watch-glasses represents the form of the cavity of the pit; and if the flattened summits were perforated, they would represent the apertures of the two pits that open into the lumen of the vessels. Further imagine that the two watch-glasses are embedded in a mass of secondary thickening, i. e. the thickness of the vessel's wall, which has been laid down, layer after layer, upon either side of the paper that extends from between the two watch-glasses until the wall is as thick as the two applied glasses, and the mental picture will be complete.

In some instances, cells become elongated, thickened and pitted, and assume other characters of vessels, but the transverse septa persist; these are called **tracheides** (Fig. 24).

All the vessels just described have their walls secondarily thickened by the deposition of layers of lignine; but there are other vessels, whose functions are different to those just described, in which the thickening, which is of cellulose and not lignine, only occurs in localized patches upon the side walls or upon the incompletely absorbed transverse septa. These vessels, on account of the sieve-like nature of the transverse septa, are called **sieve-tubes** and sometimes '**phloem vessels**' (Fig. 25). They further differ from the wood vessels, in that they still retain some of their protoplasm, though their nuclei, which is primarily one for each of the cells of which the vessel is composed, break down into a number of fragments and ultimately disappear as such. Examination of a sieve-tube (S.T) shows that it is of the nature of a long tube, the cavity of which is traversed at

comparatively short intervals by transversely arranged perforated plates (S.P), which are thicker than the longitudinal walls. These plates, called the **sieve-plates,** are the end walls of the original cells which have become thickened and perforated in a sieve-like manner, so that the cavities of the cells are in communication with each other. Not only are the cavities thus rendered continuous, but also the living protoplasm, strands of which pass through the perforations of the sieve-plates. This phenomenon of the **continuity of protoplasm** is not an uncommon one, but is often difficult of demonstration; it was first observed in sieve-tubes on account of the comparatively large size of the perforations, which renders it easy of observation. It can be most clearly seen when sections containing sieve-tubes are stained with some stain that affects the protoplasm and not the cell-wall; if such sections be treated with strong sulphuric acid in which a little Hoffman's blue is dissolved, the cellulose cell-wall and the sieve-plates swell and become transparent, while the protoplasm and its connecting strands stain blue. Fig. 25 shows a sieve-tube of the vegetable marrow thus treated. Continuity of protoplasm may be demonstrated by the same means in the endosperm of the seeds of *Strychnos Nux-vomica* and of many palms (Fig. 222); but in these instances the connecting strands or fibrils are much more delicate than is the case in sieve-tubes.

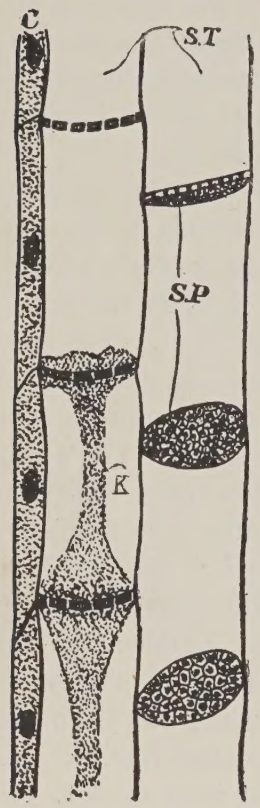


FIG. 25. Two sieve-tubes and a row of companion cells in longitudinal section, from the vascular bundle of the Vegetable Marrow. C = companion cells; K = coagulated proteid food-material, coagulated and contracted by the action of the alcoholic spirit in which the material was preserved; S.P = sieve-plates; S.T = sieve-tubes. In the right-hand sieve-tube the two lower sieve-plates are seen in surface view, since they lie obliquely towards the observer; the upper one is also partly seen in section. The three sieve-plates in the other tube are all seen in section.

Sieve-plates not only occur on the transverse walls, but also on the longitudinal walls where two sieve-tubes are in contact; they do not occur along the whole length of the wall, but in small patches, here and there. In the sieve-tubes of gymnosperms (Fig. 91, SP) and vascular cryptogams (Fig. 112, PH) these lateral sieve-plates are alone present, but then they are much more numerous; and the transverse

septa become completely absorbed, so that sieve-plates cannot, of course, be formed upon them.

The sieve-plates formed upon the transverse septa of the sieve-tubes in most herbaceous plants, such as the sunflower, bean, and vegetable marrow, are **simple** ones: that is, there is only one sieve-plate to every transverse septum, the former being coextensive with the latter; but in most woody (arboreous) plants, the secondary thickening deposited upon the transverse septa is not laid down as a single plate but as a number of plates, three or four, or more. The sieve-tubes of the lime-tree and of the grape vine, represented in Fig. 56, show such **compound sieve-plates.**

(B.) The Minute Structure of the Stem.

(*a.*) The Sunflower Stem.

If the stem of a sunflower be bisected in a median plane passing through two of the leaves, the soft tissue scraped away, and the preparation soaked for a few minutes in acid solution of aniline sulphate, there will be seen a number of yellow strands running longitudinally along the stem; these strands are the **vascular bundles.** Further examination will show that they are arranged in a circle (Fig. 28, I) in the peripheral portion of the stem, thus dividing the soft ground-tissue into an outer **cortical portion** and a central **pith.** For the most part, they run through several internodes without branching or fusing with adjacent bundles; but at every node there enters from the leaf (Fig. 26, A′, B′, C′) a variable number of veins (bundles of the leaf), usually three, which pass inwards towards the centre of the stem for a short distance only, and then turn downwards, parallel to the long axis of the stem, and fuse with some of the bundles (A, B, C) coming down from the leaves higher up; at the same time some of these bundles branch and anastomose with each other, while others pass onwards to the node next below, or to the one below that, before they branch and fuse with adjacent bundles. While, as a rule, the vascular bundles of the sunflower stem only branch at the nodes, not unfrequently lateral fusions between them occur in the internodes. The vascular bundles of the stem are thus the continuation of those coming from the leaf, so that they are common to stem and leaf; they are therefore called **common bundles.** Since the position of the portion which runs

through the stem is determined by the position of the leaf it is called a **leaf-trace.**

The arrangement of the vascular bundles in a single ring is characteristic of the stem of a dicotyledon, and clearly distinguishes it from that of a monocotyledon, in which they are arranged in a

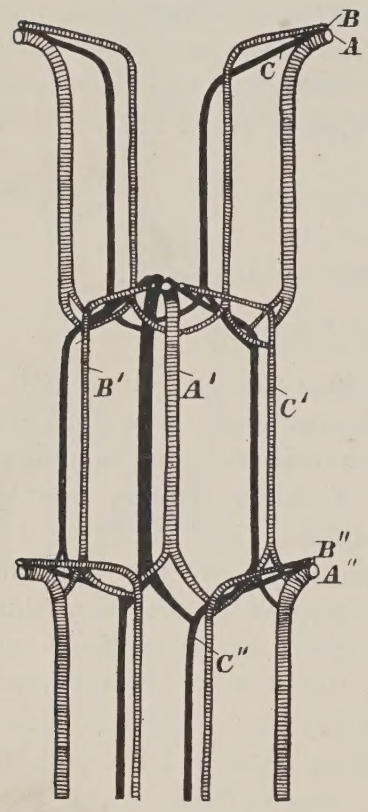


FIG. 26. Showing the course of the vascular bundles in the stem of Clematis. The bundles in the stem are arranged in the form of a cylinder, and in the figure those which are nearest the observer are shaded, while those which lie on the further side of the cylinder are in solid black. A, B, C = leaf-trace bundles coming in from the leaf; A′, B′, C′ = leaf-trace bundles coming in from the leaf at the node next below; A″, B″, C″ = leaf-trace bundles coming in from a still lower node.

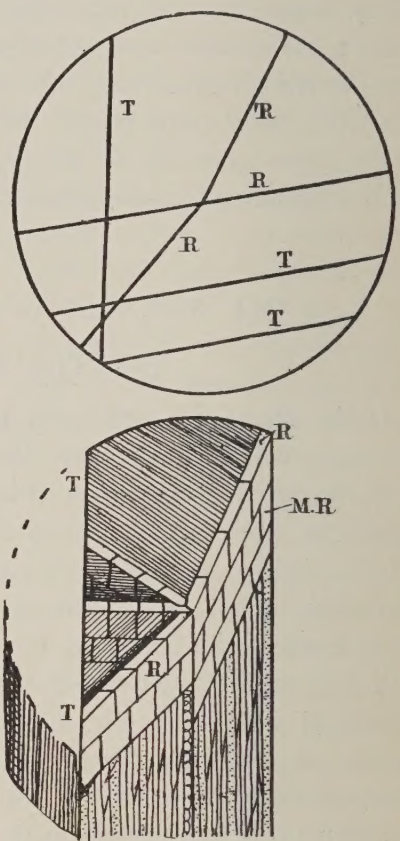


FIG. 27. Two diagrams showing the directions in which sections are made. M.R = medullary ray; R = radial sections; T = tangential sections.

more or less regular series of concentric rings. But there are some dicotyledons, i. e. *Rumex*, *Auricula*, and others, in which the various bundles coming in from the leaves are arranged in two or more concentric circles.

The arrangement of the vascular bundles in the stem of the sun-

flower, though illustrating the essential features, is not quite typical. In a typical arrangement, such, for instance, as that in the stem of *Clematis* (Fig. 26), lateral fusions occur only at the nodes, and the leaf-traces run a definite, not a variable, number of nodes before branching.

In order to investigate the minute structure of a stem beneath the microscope, it is necessary to prepare thin sections cut in the three directions of space, i. e. one transverse to the long axis of the stem, and two others parallel to it but at right angles to each other; of these two latter, the section that passes through the **organic centre** (that around which the tissues are arranged) of the stem is called the **radial section** (Fig. 27, R), and that which is taken at right angles to this, and outside the organic centre, is the **tangential section** (Fig. 27, T).

The structure of a herbaceous stem differs, in certain details, according to its age, i. e. as to whether we examine sections through the apical bud, a little below the apex, or through the middle or basal portions of the stem.

We shall postpone for the present the study of apical sections, and consider first the structure of the stem of a well-grown plant, at a little above the middle of its length.

A study of such a section shows that the stem is limited externally (Fig. 28, II, E) by a single layer of cubical or oblong cells extended here and there into little elevations, consisting of groups of cells. This investing layer of cells is called the **epidermis**, and the elevations are the bases of **multicellular hairs**, which consist of a basal portion more or less embedded in the epidermis, and continued outwards into a single series of slightly elongated cells, the terminal one of which is pointed. The walls of the epidermal cells are of cellulose, and the outer and inner walls are thicker than the lateral ones; the outermost surface of the outer wall is changed to cutin, and the continuous layer which it thus forms by confluence with that of adjacent cells, is called the **cuticle**. The protoplasmic contents are not plentiful, but chlorophyll grains are present; this is a feature worthy of notice, since chlorophyll is often absent in epidermal cells. Here and there, the continuity of the epidermis is interrupted by the presence of minute openings, the **stomata** (S), which are bounded by two special cells, the **guard-cells**, somewhat sausage-shaped in form when seen in surface view (Fig. 37, GC). The guard-cells are characterized by their more abundant protoplasm, and they serve to

increase or diminish the size of the pore by processes which we shall consider when dealing with the minute structure of the leaf.

Beneath the single-layered epidermis are several layers of a tissue characterized by the thickening of its cell-walls at the junction of three or more cells (Fig. 28, C) ; the thickening material is of cellulose, and it very frequently exhibits an obvious stratification, showing that it has been formed by the addition of successive layers. This tissue is called **collenchyma**. It forms a cylinder of somewhat rigid tissue immediately beneath the epidermis, and it is to this that the stem owes its power of resisting the stress to which it is subjected by its terminal heavy head of flowers, and the broad surface offered to the wind by the great surface of its leaves. The arrangement of the strengthening tissue in the sunflower stem is precisely that which would be adopted by the engineer, who bases his considerations upon mathematical and mechanical principles, were he to devise a structure intended to meet the same stresses. The cells of the collenchyma are elongated in the longitudinal direction (Fig. 29, C), and are approximately oblong or oval in the transverse (Fig. 28, C) ; they contain only a small quantity of protoplasm, but numerous chlorophyll corpuscles, and pass by quite a gradual transition into the thin-walled parenchyma of the cortex (CR). This latter is characterized by the thin walls and large size of its cells, the sparsity of its protoplasm, and the presence of **intercellular spaces**, formed by the splitting of the cell-wall at the junction of three or more cells ; chlorophyll corpuscles are also present.

Running through the length of the cortical parenchyma are a number of tubular organs, the **resin ducts** (Fig. 29, R), lined by a definite epithelium or membrane. They arise by the development of intercellular spaces, which become lined by an epithelial layer as the result of the division of the four primary cells surrounding the space; the cells thus arising by division become arranged into definite layers, the innermost one of which forms the epithelium. The lumena of the ducts contain resin.

Lying behind (to the outer side of) each of the vascular bundles is a strand of tissue, which consists of lignified, elongated, spindle-shaped cells, with little or no protoplasm; these are called the **sclerenchyma fibres** or **pericycle fibres** (Figs. 28 and 29, PF). When seen in transverse section they have thick walls, which in some cases are so thick that the lumen of the cell is almost obliterated;

in sections stained with hæmatoxylin the lignified walls **do not stain**, but the primary cellulose wall, called the **middle lamella**, does.

The innermost layer of the cortical parenchyma (Figs. 28 and 29, EN),

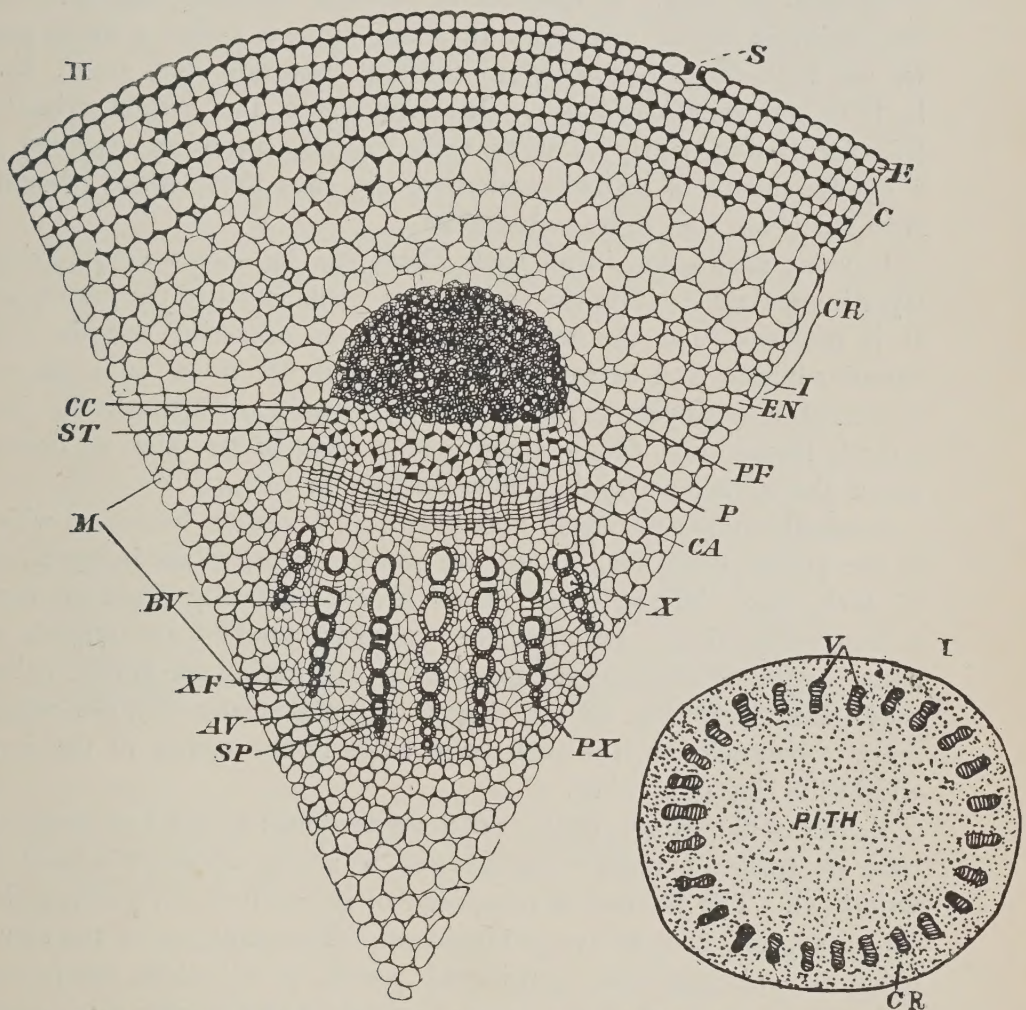


FIG. 28. Transverse section of the stem of a Sunflower (*Helianthus annuus*). I. A general view such as may be seen by cutting across the stem, smoothing the cut surface, and examining with an ordinary hand lens. II. A small portion only as seen under the one-sixth objective and magnified about 300 times. It represents a segment of I, containing one only of the vascular bundles V. AV = annular vessel of the xylem; BV = bordered-pitted vessel; C = collenchyma; CA = cambium; CC = companion cells; CR = cortex; E = epidermis; EN = endodermis; I = intercellular air-space; M = medullary ray; P = phloem or bast; PF = pericycle fibres (differentiated portion of pericycle); PX = innermost vessel of protoxylem; S = stoma; SP = spiral vessel; ST = sieve-tube; V = vascular bundles; X = xylem or wood; XF = xylem fibres.

which abuts upon the outer surface of the sclerenchyma fibres, differs in several respects from the other portion; it resists the action of sulphuric acid longer, and its radial wall possesses a band-like

thickening which appears as a black dot in sections. This layer is called the **bundle sheath** or **endodermis**; it forms a sheath investing the whole of the vascular bundles, and enclosing them in a common cylinder. A cylinder of vascular bundles, together with the pericycle fibres, medullary rays, and pith, is called a **stele**, and we see that the sunflower stem contains but one such stele: that is, it is a **monostelic stem**. In some stems, i. e. certain primulas (*Auricula*), and nearly all ferns, each vascular strand is enclosed in a bundle sheath of its own, and there are thus many steles present; such stems are said to be **polystelic**.

In some stems, and in all roots, there can be seen a very obvious layer immediately within the endodermis; this is called the **pericycle**. It is probable that the sclerenchyma fibres occurring outside each vascular bundle and between it and the endodermis in the sunflower, represent a pericycle in which the elements are differentiated into strands instead of forming a continuous layer of one kind of tissue: hence the name, pericycle fibres, applied to them.

Centrally to the pericycle fibres are the **vascular bundles**, which in the young stem, such as we are now considering, are independent of each other, but in older stems become laterally fused to form a continuous ring. Between the vascular bundles are strands of parenchyma, of the same nature as that constituting the cortex, called **medullary rays** (Fig. 28, M). These merge centrally with the central mass of parenchyma, the **pith**, which lies in the centre of the stem within the ring of bundles.

Each vascular bundle consists of three portions: an outer **phloem** (P), **bast** or **liber**; a middle **cambium** (CA); and an inner **xylem** or **wood** (X). The phloem is composed of sieve-tubes (ST), companion cells (CC), and conjunctive parenchyma. The structure of the sieve-tubes has already been considered (supra, p. 41); the companion cells (CC) are cut off from the sieve-tubes in the course of development, and form cells full of protoplasm with cellulose walls, which lie along the longitudinal walls of the sieve-tubes. In transverse section (Fig. 28), the sieve-tubes have large cavities and the companion cells appear as small, angular cells, lying in their angles. The conjunctive parenchyma is made up of thin-walled parenchymatous cells lying among the sieve-tubes, and in transverse section distinguishable from them, with difficulty, by their smaller diameters. The extreme outer portion of the phloem is known as the **primary phloem**, because, although it does not differ in structure

from the rest, except that it is smaller, it is formed by the procambial strands, derived from the apical meristem (cp. p. 74), and not from the cambium. The primary phloem is as a consequence differentiated much earlier than the rest; and of itself, its outermost portion is differentiated before its inner portion, and is called the **protophloem.** The rest of the phloem, which, as we shall later learn, is formed by cambium, may be distinguished as the **metaphloem.** Careful examination will show that the elements of the phloem, the companion cells excepted, are arranged more or less distinctly in radial rows; this arrangement is more marked in the internal layers, where the constituent elements also become smaller and thinner walled. These latter pass imperceptibly into a band of very narrow, thin-walled

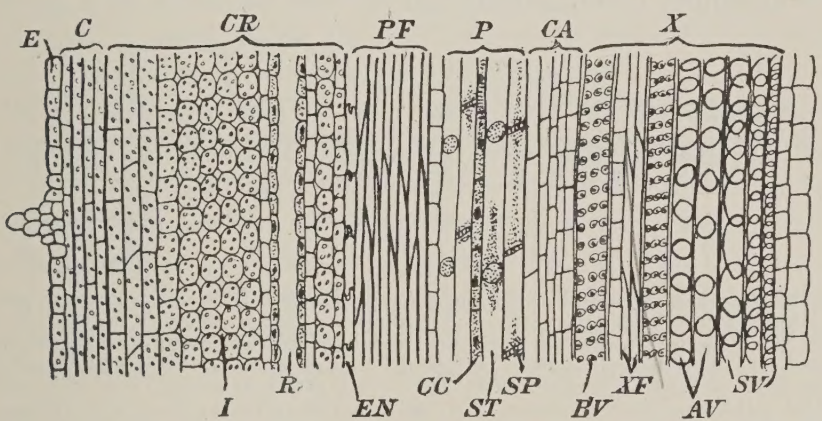


FIG. 29. Longitudinal radial section of stem of Sunflower (*Helianthus annuus*). AV annular vessels of protoxylem; BV = bordered-pitted vessels; C = collenchyma of cortex; CA = cambium; CC = companion cells; CR = remaining tissue of cortex; E = epidermis; EN endodermis; I = intercellular air-spaces; P = phloem or bast; PF = pericycle fibres; R = resin duct; SP = sieve-plate; ST = sieve-tube; SV = spiral vessels; X = xylem; XF = xylem fibres.

cells, quite regularly arranged in radial rows; this is the **cambium** (Fig. 28, CA), which is a formative tissue, and gives origin by its activity to fresh phloem on the outside, and fresh xylem on the inside. The form of each cambial cell is that of a flat, prismatic plate, with its broadest surfaces facing outwards and inwards. Seen in transverse section (Fig. 28, CA), such cells will appear as narrow, oblong ones, with their longer axes in the tangential plane, and their narrower in the radial; seen in radial section (Fig. 29, CA), they will appear as elongated narrow ones, with square ends; in tangential section they will appear as oblong plates with their transverse walls somewhat obliquely arranged.

Carefully examined in transverse section (Figs. 28 and 30), it will

be found that one row of the cambial band is narrower than the others in the radial plane ; and also that in this row some cells are narrower than others. This is due to the method by which new phloem and xylem are formed, i. e. that of cell-division. The row of cells which by continual division gives rise to others is the row with the narrowest cells; and the narrower cells among these are those which have the most recently divided. This process of the secondary formation of fresh xylem and phloem was studied by Sanio in connexion with the cambium of *Pinus*, and the law which he enunciated is usually known as '**Sanio's law.**' Briefly stated, it is as follows: one cell (Fig. 30, M) in the cambial band retains indefinitely the power of division, and is called the **initial cell** ; this cell is continually (the winter excepted) dividing into two by the formation of a periclinal

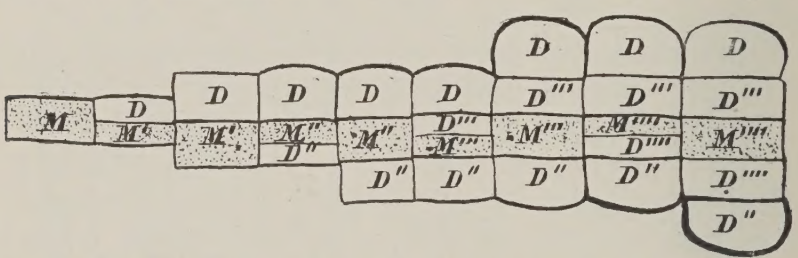


FIG. 30. Diagram of cambial division. In the living cell the changes which are here represented in lateral order take place in serial order ; that is, column 1 (to the left) would become like column 5 after two divisions, and like column 9 after four divisions had occurred. D = daughter-cell derived by first division of initial cell M ; D″, D‴, and D⁗ = daughter-cells derived by second, third, and fourth divisions respectively of initial cell; M = initial cell before first division ; M′ to M⁗ = initial cell after first to fourth divisions respectively.

wall (i. e. one arranged parallel to the surface of the stem); one of the two cells thus formed remains as an initial cell (M), and the other becomes a daughter-cell (D) ; the daughter-cell grows slightly and then divides again, but not more than once ; if the daughter-cell is divided off to the inside of the initial cell, the two cells derived from its division will form elements of the xylem, but if it is divided off to the outside, then the two resulting cells contribute to the formation of the phloem. The process is essentially the same in dicotyledons ; but whereas in *Pinus* the daughter-cell regularly and constantly divides once after it has been cut off from the initial cell, in dicotyledons this division, though it frequently takes place, is not constant.

It follows from this that we ought, in a transverse section of the stem, to be able to follow the metamorphosis of the cambial daughter-cell into phloem and xylem elements, as the case may be : and such

may be done, far easier and more convincingly in a woody stem like that of the elm or *Pinus*, but nevertheless with certainty in the herbaceous stem of the sunflower. The phloem on the one hand and the xylem on the other may be traced by gradual stages to the initial cell of the cambium, somewhat less gradually in the sunflower stem than in a woody one; for as the phloem approaches the cambium, its constituents become less like phloem elements, more like cambium; and the same is true of the xylem.

It follows also from Sanio's law that the elements of the phloem and xylem, unless subjected to subsequent disturbances, should be arranged in radial rows; and they very obviously are (Fig. 28).

A cambial tissue, then, may be identified by three very easily discernible features: the narrowness of the cells; the thinness of the walls—of the tangential walls especially; and the radial arrangement of its cells and of the elements derived from it.

Within the cambium is the xylem (Figs. 28 and 29, X), composed of from three to five, or more, very prominent rays of xylem vessels (BV, AV, SV), with xylem fibres (XF) and conjunctive parenchyma in between them. As seen in transverse section, the xylem vessels have very large cavities, the peripheral ones having the largest, and the central ones the smallest. Their walls are thick and lignified, and the middle lamella may be seen as a bright line, passing between the junction of two vessels. The smaller, more centrally situated vessels, are spiral with a tendency to become annular, and peripherally to these there are several annular vessels (AV), the innermost ones of which have their annular thickenings more widely apart than those of the outer ones. The spiral and annular vessels are not formed by the cambium, like the other vessels, but from the procambial strands formed by the formative tissue at the apex of the stem, and they are therefore formed before the cambium or the other vessels appear; they are hence called the **protoxylem**. The apical region of the stem is one of very rapid growth, and as a result of this rapidity we often find that the spiral and annular thickenings of the protoxylem are pulled out, and in some instances the vessels themselves are disorganized. A little while after the formation of the protoxylem, some of the cells of the procambial strands to the outside of the protoxylem lignify and become pitted vessels; these form the later-formed portion of the **primary xylem**, the protoxylem being the earliest formed part. Thus in the fully formed xylem strand we may distinguish between the primary and secondary xylem. The former arises from the pro-

cambial strands (p. 74), and is lignified in two stages, the earliest of which consists of spiral and annular vessels, and is called the protoxylem. The secondary xylem (metaxylem) is that part which arises from the cambium. The most externally situated vessels, with the largest diameters, are bordered-pitted vessels (BV), the pits of which, as seen in surface view (radial section), are oval in form, and arranged in horizontal lines across the width of the wall. The xylem parenchyma (conjunctiva) is restricted to the neighbourhood of the vessels around which it is arranged. The cells of which it is composed retain their protoplasmic contents, but in the case of those which surround the peripheral vessels, the cell-walls become lignified, while those in connexion with the central vessels retain their primitive cellulose walls. The xylem fibres (Fig. 28) are situated between the rays of vessels; they are long and pointed (Fig. 29, XF), and like the vessels the cell contents are absent. They are interwoven with one another, and their walls are lignified and pitted with simple pits. In life, the cavities of the vessels and fibres contain only water and gases. In addition to forming supporting structures, they also serve as the path along which water and mineral matter in solution pass from the roots to the leaves.

Examination of an older portion of the stem (Fig. 31, IC) will reveal the fact that some of the cells of the parenchyma of the medullary rays are undergoing division, chiefly by the formation of periclinal walls. This division of cells takes place in such a manner that they form a band of cambial tissue passing from the cambium (C) of one bundle to that of another; and since this occurs in the medullary ray between every bundle, there arises a continuous ring of cambium, upon the inside of which new xylem will be formed, and new phloem on the outside. The cambium thus formed between the bundles is called **interfascicular cambium**, and, as already indicated, it becomes continuous with the **fascicular cambium**, or cambium within the bundle.

The result of the activity of the interfascicular cambium is the formation of a ring of wood (Fig. 31, X′) on its inner side, and of phloem (P′) on its outer; but the ring is not continuous, for it is interrupted by the presence of narrow, parenchymatous strands (M′), which extend from the pith (P) to the cortex (CR). These are medullary rays, and they differ from the medullary rays which separate the primary bundles in their structure and in the fact that they have arisen from the cambium; for while the cambium is forming new

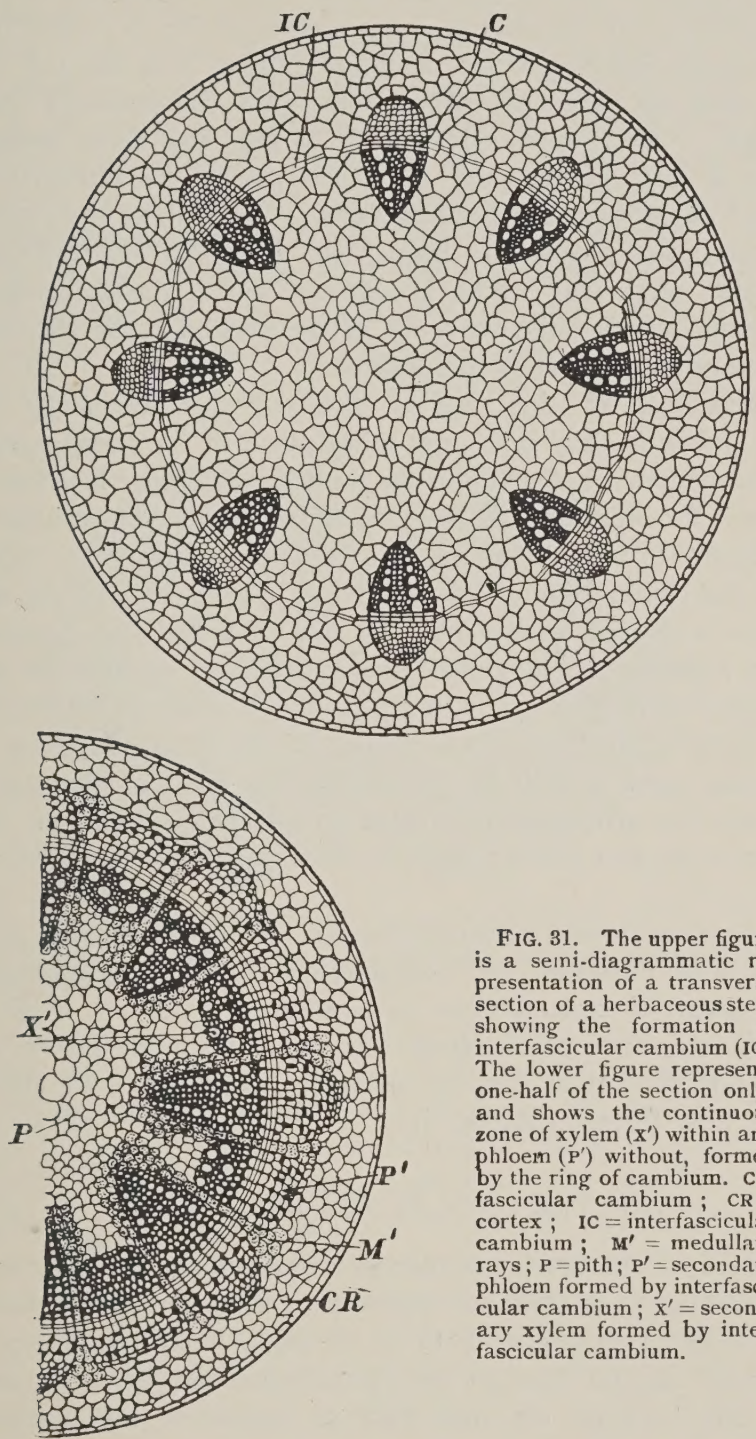


FIG. 31. The upper figure is a semi-diagrammatic representation of a transverse section of a herbaceous stem showing the formation of interfascicular cambium (IC). The lower figure represents one-half of the section only, and shows the continuous zone of xylem (X') within and phloem (P') without, formed by the ring of cambium. C = fascicular cambium ; CR = cortex ; IC = interfascicular cambium ; M' = medullary rays ; P = pith ; P' = secondary phloem formed by interfascicular cambium ; X' = secondary xylem formed by interfascicular cambium.

xylem and phloem elements, it also forms the parenchymatous strands that constitute the medullary rays. Some of the rays which thus arise from the interfascicular cambium extend from the pith to the cortex; these are called **principal** (sometimes also **primary**) **medullary rays.** Others only extend part of the way from within the xylem to a part of the way outwards within the phloem; these are called **secondary medullary rays.** The cells of the medullary rays retain their protoplasm throughout life; but the cell-walls of that portion of the ray which is situated within the xylem become lignified and pitted, while the walls of the portion in the phloem and cortex retain their cellulose composition.

The formation of this ring of interfascicular secondary xylem, phloem, and medullary rays only takes place in the basal portion of the sunflower stem; higher up in the middle portion, the interfascicular cambium is formed, but little or no interfascicular xylem or phloem.

The sunflower stem does not live beyond its first year; but if it did, and the cambium renewed its activity in the spring of the second year, there would be formed another ring of xylem and phloem. If this were repeated through successive years there would result a stem with concentric rings of xylem and phloem; in other words, we should have a type of structure characteristic of an arboreous stem. And just as the basal portion of the herbaceous stem of the sunflower approaches the arboreous condition, so all arboreous stems, in the early part of the first year of their existence, pass through a herbaceous stage.

All arboreous stems, towards the end of the first year of their existence and onwards, are characterized by the presence of an external layer of cork, formed in a manner which we shall study later. At the base of the sunflower stem, a similar brown, corky layer is formed, but as this is not typical of herbaceous stems we shall not now further consider it.

(*b.*) The Stem of the Bean-plant.

The stem of the scarlet runner is a very elongated one, and we shall learn that its internal structure differs from that of the sunflower stem in a way that adapts it to its climbing habit. If we examine a transverse section through the epicotyledonary portion (that part of the axis between the first pair of vegetative leaves and the cotyledons) of a very young seedling plant, younger than that figured

in Fig. 3, we shall find that in its principal features it resembles the apical part of the sunflower stem ; for there is an external limiting epidermis (Figs. 32 and 33, E), containing stomata (S), with a large-celled parenchymatous cortex (CR) within ; the outer layer of the cortex is composed of much smaller cells, and may be distinguished as a hypodermis, while the innermost layer consists of more regularly oblong cells containing starch, and constitutes in the young stem a very definite endodermis (EN). The stem is monostelic, like that of the sunflower and of nearly all phanerogamous stems, and in the very young stem which we are considering the vascular bundles are separated from each other by relatively broad bands of parenchyma, the medullary rays. But in a slightly older stem, such as that

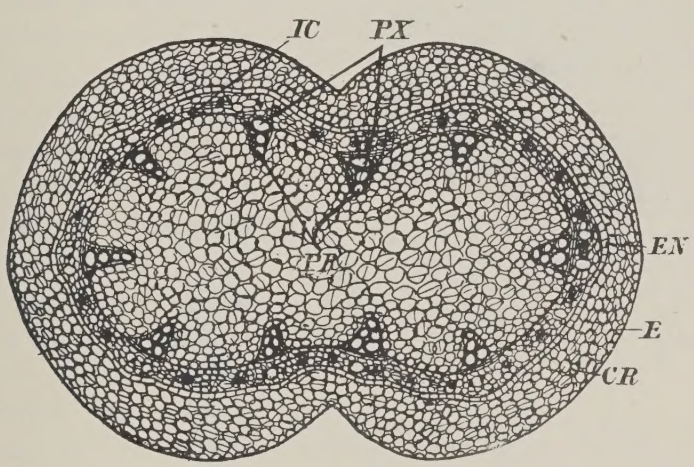


FIG. 32. Transverse section of the stem of a seedling Bean-plant, taken through the plane A–B indicated in Fig. 3. Magnified 70 times. CR = cortex ; E = epidermis ; EN = endodermis ; IC = interfascicular cambium, here very early developed ; PR = protoxylem ; PX = outer portion of primary xylem.

figured in Fig. 3, even if the section be made immediately behind the apex, as in the plane A–B, we shall find that already the interfascicular cambium (Figs. 31 and 32, IC) is formed, so that a complete ring of cambium extends round the stem. Within the cambial ring and occurring at regular intervals are the xylem strands, composed centrally of the protoxylem (Figs. 31 and 33, PR), consisting of an innermost spiral vessel with an annular one immediately without that, and peripherally of a few very large, bordered-pitted vessels of the later formed primary xylem (PX). Without the cambium ring are the primary phloem strands, not confined, as in the sunflower and as is usually the case, to strands corresponding in number to the primary xylem, but occurring very much more numerously. Behind each

xylem strand, and not infrequently alternating with them, there occur very large vessels (Fig. 33, PP′) which in transverse section show thickenings of part of their side walls; in longitudinal section they are seen to be cells with sieve-plates on their lateral walls (Fig. 33, II, SP), and possibly represent the protophloem.

Within the endodermis (EN) is a ground-tissue composed partly of prosenchyma and partly of parenchyma; in an older stem (Fig. 34, PF) the prosenchyma cells become lignified and form strands of sclerenchyma, which from their position are regarded as differentiated portions of the pericycle.

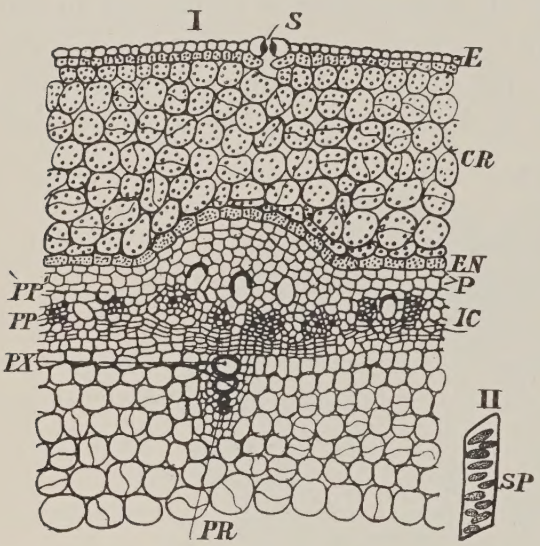


FIG. 33. I. A small portion of the section figured in Fig. 32, more highly magnified (about 300 times). CR = cortex (extra-stelar tissue); E = epidermis; EN = endodermis; IC = interfascicular cambium; P = pericycle; PP = primary phloem; PP′ = large cells with lateral sieve-plates, and probably representing the protophloem; PR = protoxylem; PX = outer part of primary xylem; S = stoma. II. One of the large cells PP′, seen in side view; SP = sieve-plates.

In a young stem such as that of the seedling we are considering, many of the cells of the cortex and pith multiply by division, in order to keep pace with the rapid increase in the size of the stem; this is a condition which very early ceases, and is not found in a slightly older stem.

After the formation of the interfascicular cambium, a zone of secondary xylem, consisting of thick-walled xylem fibres with small cavities, is formed by the growth and modification of the cells derived from it (Fig. 34, X′). The object of this is to attain rigidity consistent with a very considerable amount of flexibility, for a climbing stem must be flexible and there must be as much rigidity as possible in order to give it support. This is followed by the formation of a much broader band of xylem (X), consisting of relatively large xylem fibres (XF), xylem parenchyma (XP), and large xylem vessels (XV) of the bordered-pitted type. Simultaneously with the production of the secondary xylem on the inner side of the cambium ring, secondary phloem (Fig. 34, SP) is formed on its outer side; this consists of sieve-tubes (ST), companion cells, and phloem parenchyma,

and is of the same nature and constituted of the same constituents as that in the sunflower.

The cambium ring not only forms secondary xylem and phloem, but at approximately equidistant intervals it also produces, both on

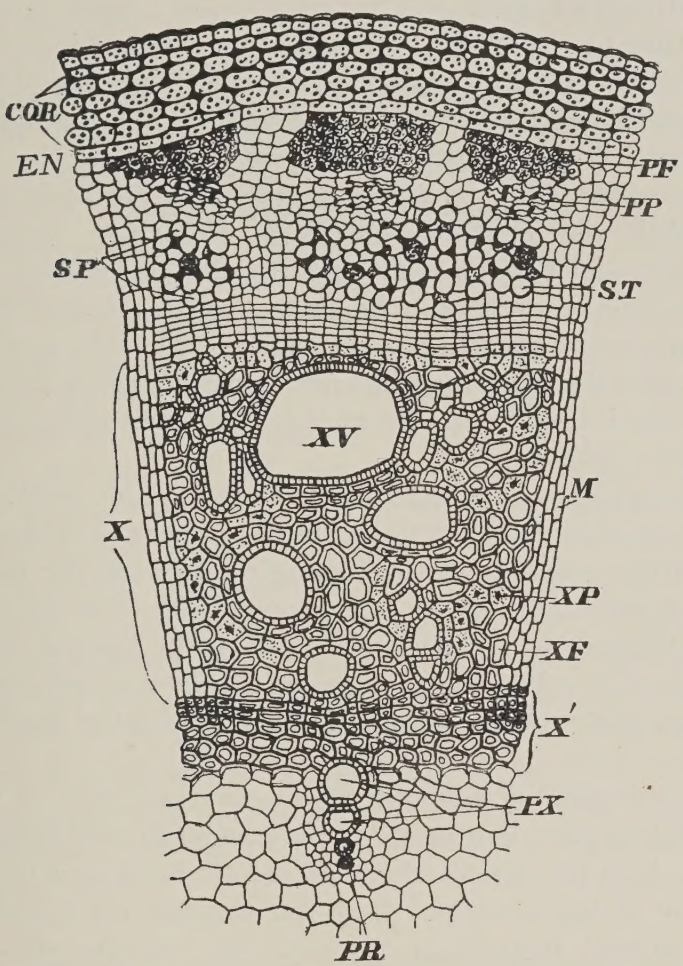


FIG. 34. Segment of a transverse section of an older (climbing) stem of the Bean-plant (*Phaseolus*). Magnified 300 times. COR = cortex; EN = endodermis (innermost layer of cortex); M = medullary ray; PF = pericycle fibres (differentiated portion of pericycle); PP = primary phloem; PR = protoxylem; PX = outer portion of primary xylem; SP = secondary phloem; ST = sieve-tube; X = secondary xylem; X' = early formed portion of secondary xylem; XF = xylem fibre; XP = xylem parenchyma; XV = xylem vessel. The epidermis and the cambium are not lettered. The cambium is the zone of narrow cells between SP and X.

its inner and outer surfaces, strands of parenchyma, which pierce the thickness of the xylem and phloem, and serve to place the pith in connexion with the cortex; these strands are called **medullary rays**, and they occur at all levels along the whole length of the stem. In the bean-plant they are some two to three layers of cells in

thickness and some four to six in depth ; the cells contain copious protoplasm, and relatively large nuclei.

In the climbing stem such as we are now considering, the pericycle fibres (PF) are lignified and very thick-walled ; obviously these strands of strengthening tissue give considerable rigidity to the stem and at the same time allow of a certain degree of flexibility, more than could be obtained if there existed a continuous cylinder of lignified tissue in place of the strands ; and, moreover, they form hard protective structures outside the nutritive conveying vessels of the phloem, a very necessary condition in climbing stems that are liable to injury in forcing their way upwards through other plants. Between the pericycle fibres and the secondary phloem, the crushed constituents of the primary phloem (PP) can be seen ; upon the formation of the secondary xylem and phloem the stem increases rapidly in its radial dimensions, with the result that the primary phloem which lies between the bulk of the increasing tissues and the hard, unyielding pericycle fibres becomes crushed.

The climbing stem, as distinguished from that of the seedling stem, is further strengthened by the thickening of the angles of the cells of the cortical tissue (COR) ; this thickening results from the deposition of cellulose in the angles of the cells in such a way that the cell-wall becomes thickened at the point where it is in contact with two or more adjoining cells, but not where it is in contact with only one ; there is thus produced an additional tissue possessing rigidity with flexibility.

If now we compare the stem of the bean-plant with that of the sunflower, we shall see that they resemble one another in their fundamental features : in both the vascular bundles are arranged in a circle near the periphery of the stem, and they run through the length of the internodes without branching ; in both the vascular strands are **open and collateral bundles**, i. e. they contain cambium, and the phloem lies to the outside of the xylem and on the same radius, respectively ; in both the vascular bundles are enclosed in a common endodermis, so that the stem in either case is **monostelic**, and in both the xylem constituents include vessels as well as fibres and parenchyma.

When we contrast the two stems, we find that such differences as they exhibit are correlated with the differences in their habits. The sunflower stem at the time of flowering is subjected to great stress in virtue of the weight of the large terminal flowers, and on

breezy days on account of the large expanse of its leaves; but its diameter compared to its height is after all not very disproportionate, and the stresses to which it is subjected are met by the formation of the collenchymatous zone within the epidermis, and of the pericycle fibres and the xylem strands within that. With the bean-plant stem, the case is different, for it is unable to maintain itself erect without some support, since its length as compared to its diameter is enormous; the requisite support it obtains by coiling round other bodies, a habit of existence which demands a certain rigidity of parts combined with great flexibility. Both these qualities are required to prevent kinking of the thin-walled sieve-tubes and of the thicker xylem vessels, a condition of things which would be incompatible with the discharge of those functions that are necessary for the maintenance of the life of the plant. Hence we find in the stem of the scarlet runner, that the interfascicular cambium is formed very much earlier than is the case with the sunflower stem, in order that the flexible rigidity so necessary for the plant shall be quickly obtained by the formation of a complete circle of strengthening tissue in the form of secondary xylem. Moreover, a climbing stem must climb rapidly upwards if it is to obtain full advantage of the habit, so as to possess, undiminished by the shadows and requirements of rivals, the full benefit of light and air; but rapid climbing means rapid growth, and growth is the result of the continuous assimilation of food-material, and this is in part supplied by the sap which circulates upwards from the root to the leaves, through the channels of the xylem; hence the necessity, apart from the rigidity conferred, of the earliest possible formation of as much secondary xylem as the requirements of the plant may demand.

(C.) The Minute Structure of the Leaf.

(*a.*) The Sunflower Leaf.

The general form and characters of the leaf have already been considered (supra, p. 9). In minute structure, it is composed of the same tissues as those forming the stem, but differently arranged.

The structure of the petiole resembles in many respects that of the young stem, but differs from it in its form, which is semilunar, not cylindrical, its flattened or concave face being uppermost, and its rounded one undermost; the vascular bundles are not arranged in a circle, as in the stem, but in an arc, which corresponds in form and

extent to the rounded under surface of the petiole. Interfascicular cambium is never formed, and fascicular cambium is alone found in the larger of the bundles, and even in these only for a limited time. There are, as a rule, three principal bundles and several smaller ones. The petiole, unlike the stem, is polystelic, each bundle being surrounded by its own bundle sheath. In the epidermis, the stomata are more numerous than is the case in the stem, and beneath each stoma the collenchyma is replaced by thin-walled, chlorophyll-containing parenchyma, with large intercellular air-spaces.

Examination of sections made parallel to the surface of the lamina (Fig. 35) shows that many of the ultimate branchlets of the veins (V) end blindly in the parenchyma filling the meshes, and that some of them pass outwards to the margin of the leaf, and terminate in its teeth-like projections.

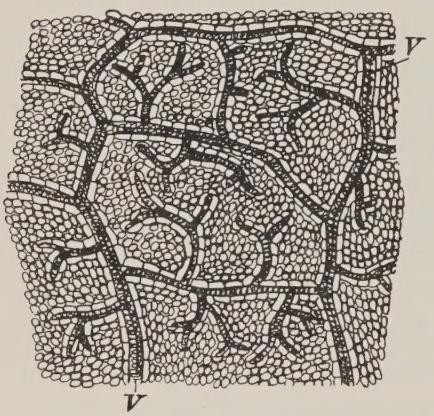


FIG. 35. Section of a leaf of the Sunflower (*Helianthus annuus*), taken parallel to the surface to show the branching and mode of termination of the vascular bundles (veins), V.

Examination of a transverse section of the lamina (Fig. 36), made across and accurately at right angles to one of the principal veins, will show the following arrangement of its tissues: the section has an undulating, though in the main uniform breadth of form; the upper surface is limited by a single-layered **epidermis** (E), covered externally with a thin cuticle; the epidermal cells are of the same form as those of the stem, and some of them bear a number of multicellular hairs (H), similar to those of the stem. Beneath the epidermis is a two-layered row of elongated cells (P), with their long axes perpendicular to the surface of the leaf, and containing copious protoplasm and chlorophyll corpuscles; this tissue is called the **palisade parenchyma.** Abutting upon its under surface, is a tissue composed of irregular, parenchymatous cells (SP), characterized by its large intercellular spaces, and called the **spongy parenchyma.** This latter tissue and the palisade parenchyma are grouped together under the general term of **mesophyll.** The lower surface of the section is bounded by the epidermis (E), which possesses the same characters as that of the upper one, and differs from it alone, in that it has much more numerous stomata.

The vascular bundles of the leaf are similar to those in the younger parts of the stem, but contain no cambium; the leaf when once formed

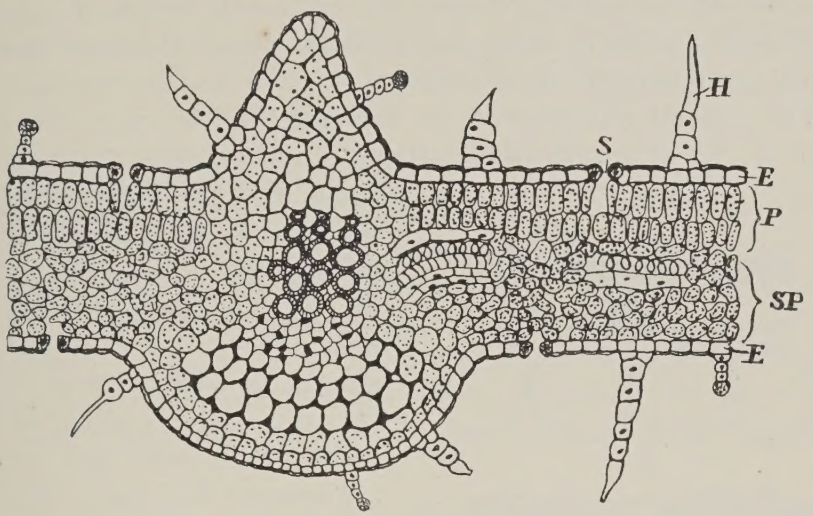


FIG. 36. Transverse section of the leaf of Sunflower (*Helianthus annuus*), passing through a vein. E = epidermis; H = multicellular hairs; P = palisade parenchyma; S = stoma; SP = spongy parenchyma. The leaf is thickened in the region of the vein—on the upper surface by a strand of parenchyma, and on the lower by collenchyma. The tubes with spiral and annular markings passing through the right half of the section are the xylem vessels of a small vein, branching off from the principal one in the middle.

does not increase by the addition of new tissues, and so does not need an actively dividing tissue. The xylem of the bundles always faces

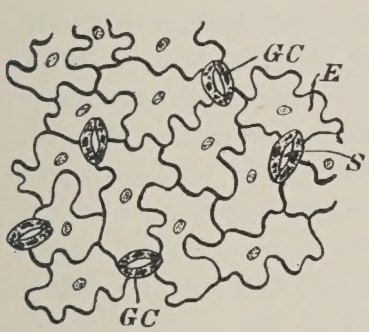


FIG. 37. A piece of the epidermis of the leaf of the Sunflower stripped off and examined in water under the one-sixth objective, to show the form of the epidermal cells and the stomata. E = epidermal cell; GC = guard-cells; S = stoma.

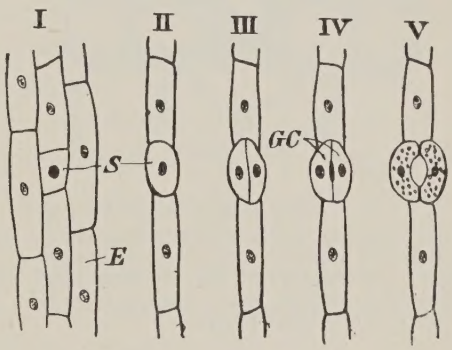


FIG. 38. Preparations of the epidermis of the leaf of the Hyacinth to show the origin and development of the stomata from epidermal cells. E = epidermal cell; GC = guard-cells; S = cell cut off from an epidermal cell and destined to form the guard-cells of the stoma.

the upper surface of the leaf, and the phloem the under surface; this constant condition is the necessary result of the fact that the xylem in the stem is innermost and the phloem outermost, and that the bundles

turn outwards to the leaves without undergoing any twisting. As we trace the bundles of the leaves to their finer ramifications we find that they assume a simpler structure, and ultimately consist of a few spiral tracheides and sieve-tubes, and even the latter disappear before the actual termination of the bundle.

The general structure of the stomata (Fig. 36, S) is the same as that of the epidermis of the stem; in section the **guard-cells** are small, and just internally to them is a definite space, the **respiratory cavity.** Seen in surface view (Fig. 37, GC), the guard-cells are elongated and curved in form, and lie among the ordinary epidermal cells (E); these latter contain no chlorophyll grains, while the guard-cells are crowded with them. The guard-cells, by alteration of their form, can enlarge or diminish the size of the stoma, and thus prevent or increase the amount of transpiration (infra, p. 456).

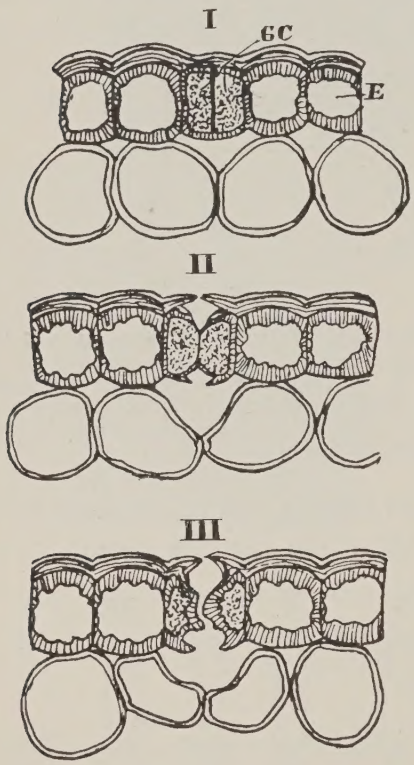


FIG. 39. Three stages in the development of the stomata in the leaf of the Hyacinth, as observed in transverse sections. E = epidermal cell, showing thick stratified cuticle and sinuous internal surface; GC = guard-cells.

The guard-cells are derived from the ordinary epidermal cells, and as their development may be very easily followed in the leaf of the hyacinth, we shall describe it as it occurs in that plant. If we strip off a piece of the epidermis from the apical part of a young hyacinth leaf, mount it in a drop of water, and place it under the microscope, we shall find that it is composed (Fig. 38, I) of elongated epidermal cells devoid of chlorophyll grains; at the end of some of these cells we shall find that a small one (S) has been cut off by the formation of a transverse wall. At first it grows slightly (II), then it divides into two (Fig. 38, III, and Fig. 39, I), each of which will later become the guard-cell of a stoma, and there begins to be formed between the two cells a small opening or cleft, which at first is confined to the upper and lower surfaces of the two cells (Fig. 38, IV, and Fig. 39, II); the

cleft enlarges and the two guard-cells become curved in form as seen in a surface view, but in transverse section they have a peculiar form, the result of which is to render the passage between them somewhat sinuous (Fig. 38, V, and Fig. 39, III). At this stage they develop chlorophyll grains, and become functionally active organs.

(*b.*) The Bean-plant Leaf.

In its minute structure the leaf of the bean is very similar to that of the sunflower, and the same description and figures will answer for both. There is only one minor difference of detail, for in the bean leaf there is for the most part only a single layer of palisade parenchyma (Fig. 36, P), and not two as in the sunflower leaf. The same kinds of epidermal hairs are present on the upper and under surfaces of both leaves, and stomata are present in both upper and under epidermal layers.

(*c.*) Holly Leaf.

The structure of the leaf of the bean and sunflower plants, though typical of that of a dicotyledonous leaf, is not one that is invariable, so it will be necessary to study that of some other leaves.

The leaf of the holly (*Ilex aquifolium*) has a leathery lamina, with a spiny margin of cartilaginous texture, and a short, cylindrical petiole, with no stipules. It has a reticulate, unicostate venation.

Examination of a transverse section, taken across one of the lateral veins, shows in general the same structure as that of the sunflower or the bean, but also certain additional tissues.

The upper epidermis (Fig. 40, E) is composed of a single layer of square or oblong cells with no chlorophyll, and with thick walls, the lateral ones of which are pitted, while the outer one is differentiated into three distinct layers: an outer, thick cuticle (C), a cellulose layer partly cuticularized, and an unaltered cellulose layer abutting on the cell cavity. The cuticle is, therefore, derived from the altered cellulose wall by a chemical modification of it, accompanied also with physical changes. Stomata are absent. Within the epidermis is a strengthening tissue, the **hypodermis** (H), which is absent in the sunflower and bean-plant, consisting of a single layer of cells with fairly thick, cellulose, pitted walls; over the midrib the hypodermis is two layers thick, and along the margins of the leaf it may become three or four layers thick, and is here also strengthened by a mass of sclerenchyma immediately beneath it (Fig. 40, I, S).

Beneath the hypodermis are three layers of elongated cells, the palisade parenchyma (P); they have the same characters as that in the sunflower, but here and there some of them have their protoplasm reduced and enclose a large crystal; these crystal-containing cells are called **idioblasts**. The spongy parenchyma (SP) is similar to that of the sunflower, but it contains several idioblasts. The lower epidermis (E) is similar to that of the upper surface, and like it bears no hairs; it differs from the upper epidermis in the thinness of the cuticle

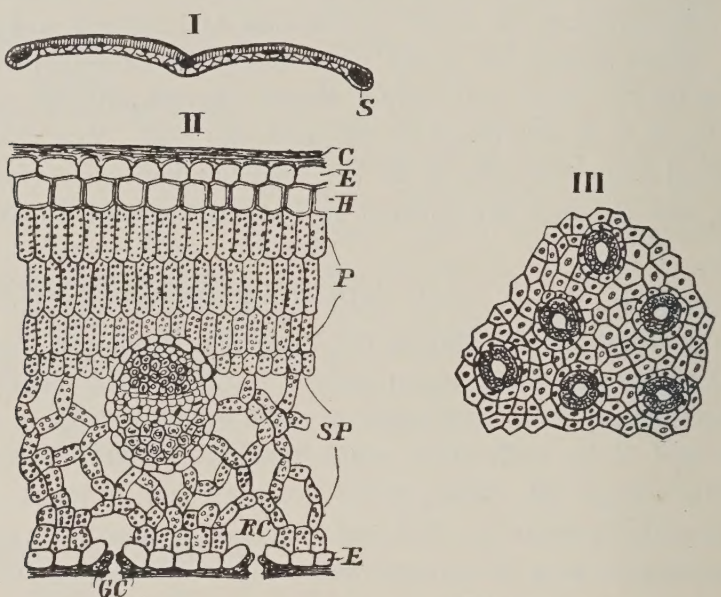


FIG. 40. I and II. Transverse sections of the leaf of Holly (*Ilex aquifolium*). III. Surface view of the epidermis from the under surface. I. As viewed under a low power (two-third objective), and the section of the whole width of the leaf represented. II. As observed under a high power (one-sixth objective), and a small portion only of the section with a vein represented. C = cuticle; E = epidermis; GC = guard-cell; H = hypodermis; P = palisade parenchyma; RC = respiratory cavity; SP = spongy parenchyma. The vein is surrounded by an endodermis, and its constituents from below upwards are: sclerenchyma, phloem, xylem.

and in the presence of stomata (GC and III). The two guard-cells (GC) lie somewhat below the surface, contain chlorophyll, and project into the aperture in a ridge-like manner; the cuticle also passes in over the guard-cells into the pore of the stoma. Internally to the stoma, and just over it, is a large intercellular space belonging to the spongy parenchyma, and called the **respiratory cavity** (RC).

As in the sunflower, the vascular bundles ramify in the leaf at the junction of the palisade and spongy parenchyma; in the large bundle of the midrib, and sometimes in the smaller lateral ones, cambiform cells can be observed between the phloem and the xylem.

The leaf of the holly thus differs from that of the sunflower in the absence of hairs, and of stomata from the upper surface; in the greater thickness of the cuticle, and in the presence of a hypodermis and a marginal strand of sclerenchyma.

These differences are correlated with the differences in the conditions under which in nature the two plants live. The holly belongs to an Order that lives in the tropics and in the dry regions of central Asia and in western and southern Europe, where it is liable like other plants to the ravages of animals and to periods of drought. Obviously the marginal strand of strengthening sclerenchyma forming a base for the row of cuticularized spines is an advantage to the plant, in so far as it renders it obnoxious to plant-feeding animals; for actual observations (by Charles Darwin) have shown that although all conditions requisite for the propagation of a race of plants may be present, if the plants in virtue of their own structure or acrid nature of their juices are not protected against the attack of animals, they may be eaten as fast as they appear above the surface of the ground, and the propagation of the race in that particular locality altogether prohibited; while if they be protected, as by being fenced in, they will at once flourish luxuriantly and procreate their species. The presence of the thick, vapour-impenetrable cuticle on both upper and under surfaces of the leaf is of advantage, since it prevents evaporation of the water in the leaves—which are the food factories of the plant and dependent upon the presence of water, among other things, for the discharge of their functions—other than through the stomal pores, which possess a controlling power over the amount of water transpired under varying conditions. It can thus live through periods of drought when other plants with thinner cuticle on their leaves would perish. Moreover, the thicker the cuticle the more difficult it is for insects to deposit their eggs within the surface of the leaf, and for the larvæ which develop from them to bore their way inwards to the vital tissue of the organ. Thus the holly is adapted to live under conditions which would be unfavourable to the sunflower, and so in the struggle for existence created by the tendency of organisms to multiply beyond the means of subsistence, the holly may flourish where others will perish; but should the conditions alter, or if the holly endeavoured to make a stand where its structure did not adapt it to its conditions, or it itself failed to produce a progeny capable of structural and physiological adaptation to altered circumstances, then its race would perish and others better

adapted would survive. Thus it is that the holly and sunflower are adapted to their own conditions of life, not because they have been intelligently made to fit the conditions, but because in the course of time they have varied in directions which render them fit to exist under the given conditions, and because those unfitted have become eliminated. With plants as with animals, to live is to struggle for existence; the fit survive, the unfit are eliminated.

(*d.*) Leaf of the Stonecrop (*Sedum acre*).

The leaf of the stonecrop is a **concentric leaf**, and is so called because its tissues are arranged concentrically around a central axis; those so far studied are bifacial ones, possessing an upper and under surface and with their tissues arranged in layers. Concentric leaves are usually found on succulent plants, and the distinction into upper and under surface is not structurally indicated, since the tissues are concentrically arranged around the vascular bundles.

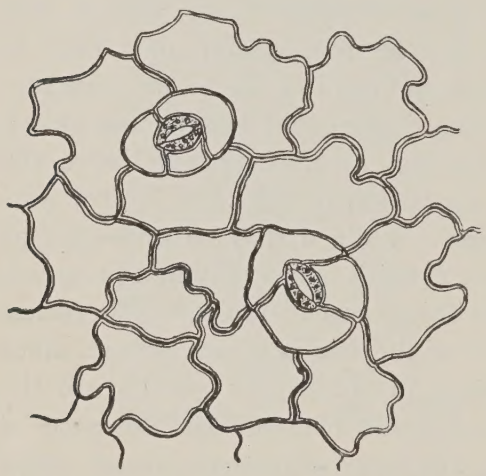


Fig. 41. Surface view of the epidermis of the leaf of the Stonecrop (*Sedum acre*), showing the three subsidiary cells surrounding the stoma.

The leaves of the stonecrop are small, somewhat cylindrical in form, and taper to a blunt apex; they are sessile upon the stem (directly attached without a petiole). In transverse section the outline is even and oval, and hairs are absent. The epidermis is a single layer of cells, with small stomata and a well-defined cuticle. Within the epidermis the bulk of the leaf is occupied by mesophyll, composed of rounded, thin-walled, chlorophyll-containing cells, with somewhat scanty protoplasm and a large central vacuole. Intercellular spaces are numerous but not large. Traversing the centre of the leaf are three or four small vascular bundles containing xylem and phloem, but no cambium.

The stomata, though small, are more complicated than any hitherto considered. Seen in surface view (Fig. 41), as when a piece of epidermis is stripped off and examined in water, the pore of the stoma is observed to be bounded on either side by a nucleated chlorophyll-containing

guard-cell, and they are surrounded by three **subsidiary cells**, differing in size and shape from the ordinary epidermal cells, which are sinuous in outline and contain no chlorophyll. The subsidiary cells are developed from the same parent cell as the guard-cells of the stoma, and their origin will be better understood by reference to a simpler case than that of the stonecrop, such as that of *Tradescantia* (Fig. 42, SC). When the parent cell divides into two cells, each of these does not immediately become a guard-cell as in the case of the hyacinth, but divides again in the same plane. Upon the formation of the pore there are then two cells on either side of it, an outer and an inner; the latter becomes the guard-cell and the former the subsidiary cell of the stoma.

The stonecrop is a plant which lives on dry rocks and stony places, and in consequence may be often for long periods at a time without a supply of water. Hence it is necessary that all surfaces from which evaporation might take place should be reduced as much as is consistent with the performance of the general functions of the plant. We accordingly find that the form of the leaf is one where the minimum amount of surface and the maximum amount of cubical capacity within—which is occupied by water-containing tissue—is attainable, for a cylindrical body conforms to these conditions. The presence of the well-defined cuticle is a means to the same end. Thus the plant is adapted to take up as much water as it can when rain falls, and to reserve it for use during periods when no rain is falling.

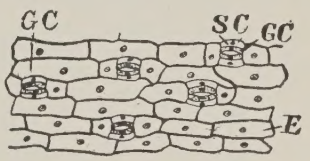


FIG. 42. Surface view of the lower epidermis of *Tradescantia*. E=epidermal cell; GC=guard-cell; SC=subsidiary cell.

(D.) THE MINUTE STRUCTURE OF THE ROOT.

(*a.*) THE ROOT OF BEAN (*Phaseolus*).

The internal structure of the root, like that of the stem, varies with its age. Examination of a transverse section taken through the root below the origin of the last of the lateral rootlets, somewhere between them and the apex, will show that the root at this stage (Fig. 43) is limited externally by a not well-defined layer, the **epidermis**, or better called, the **piliferous layer** (P.L), consisting of somewhat flattened, oblong cells, some of which are prolonged outwards into filamentous processes, the **root-hairs** (H). These are, therefore, unicellular, and

they come into very intimate contact with the particles of the soil, absorbing what mineral matter may be dissolved in the film of water surrounding the grains. Within the piliferous layer is the **cortex** (CR), which, relatively to the diameter of the root, is very wide; it consists of several layers of thin-walled parenchyma with intercellular spaces.

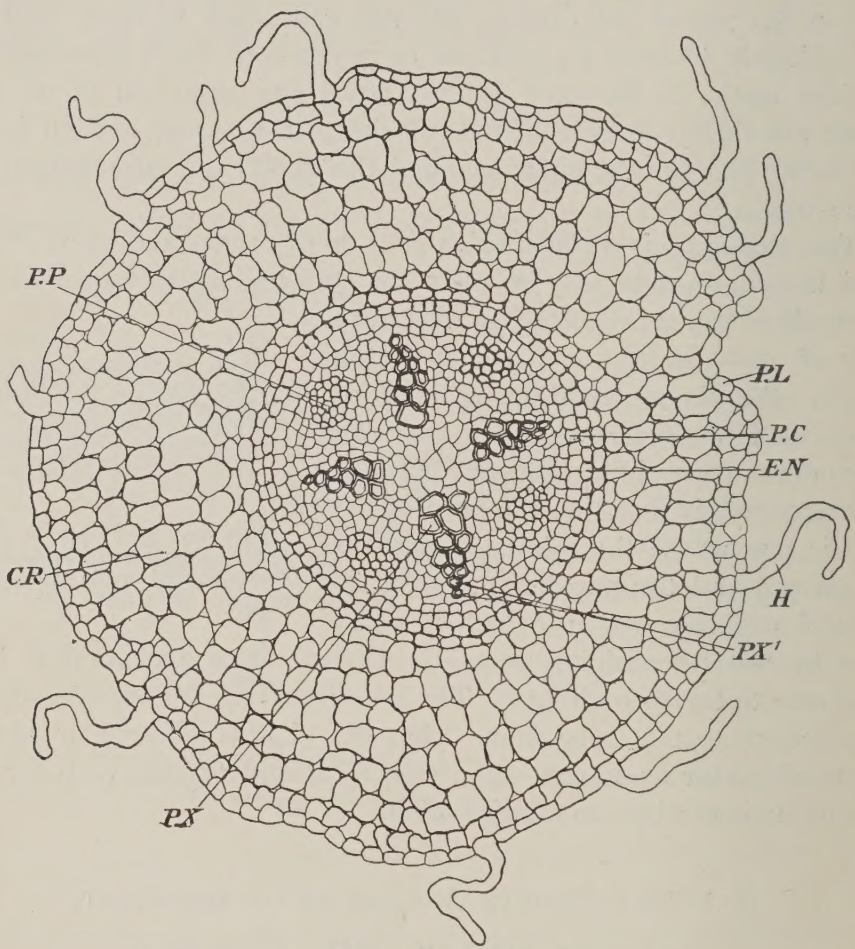


FIG. 43. Transverse section of the root of Bean (*Phaseolus multiflorus*), taken through the root-hair bearing region. CR = cortex; EN = endodermis; H = root-hair; P.C = pericycle; P.L = piliferous layer; P.P = primary phloem; PX = primary xylem; PX′ = protoxylem.

The **endodermis** (EN) limits the cortex internally, and is composed of a single layer of cells, somewhat cubical in form, and possessing a dark dot on the radial walls; this dot is due to reflection of the light which occurs from every fold of the folded radial walls. Within the endodermis is the **pericycle** (P.C), which consists, for the most part, of a single layer of cells, thin walled, and arranged in an undulating

band; opposite to the xylem it may be two or three layers in thickness. Within the pericycle and occupying the centre of the section is a ground-tissue, divided into a central **pith** and bands of parenchyma lying between the phloem (P.P) and xylem (PX) strands. The xylem in a root at this stage consists of four strands of **primary xylem** (PX), with a radiate arrangement; dependent upon the exact stage of development, the primary xylem may be greater or smaller in amount, but usually new primary xylem elements may be seen thickening within (centrally to) that already formed; the first formed portion of the xylem, the **protoxylem** (PX′), which consists of spiral vessels, is thus situated at the *outside* of the primary xylem, which is formed a little later by lignification of thin-walled elements within. The root thus differs from the stem in that the development of its primary xylem is **centripetal**, and not **centrifugal**. Alternating with the four primary xylem groups are four primary phloem groups (P.P), and lying somewhat a little outwardly to the primary xylem; they are not, as a rule, well marked, and are separated from each other by broad bands of parenchyma; their development is like that of the phloem of the stem and the xylem of the root, i. e. centripetal.

The root thus differs from the stem in the centripetal development of its primary xylem, and in the arrangement of its vascular tissues, for in the latter the phloem lies on the same radius as the xylem, constituting a collateral bundle, while in the root it alternates with it, and the bundle is, therefore, called a **radial** one. The root further differs in that it has a wide cortex, while the stem has a narrow one; and in that its pith is very small, and in most cases is absent, but in the stem it is very large.

Examination of an older root, as of a section taken somewhere through the region of the lateral rootlets, but avoiding them, will show the primary xylem and phloem much more developed (Fig. 44), and also, that the parenchyma that lies to the central side of the phloem has commenced to divide by tangential walls, and is becoming, or has become, an active cambium (C). The cambium soon extends and forms a complete ring lying between the primary phloem and xylem strands. In a much older root, there will have been derived from this cambial ring **secondary xylem** and **phloem**, the former of which consists of four wedges lying between and without the primary xylem, while the latter lies between the primary phloem and secondary xylem, but has been displaced by being carried outwards, relatively to its position with respect to the primary xylem.

In a section where the cambial ring has just commenced to develop, it will be found that another cambium, the **cork cambium**, has commenced to form; this arises by the formation of periclinal walls in the cells of the pericycle, and from it there is developed several layers of cork cells. Since cork is impervious to gases or water, it follows that all tissues without this layer become cut off from the food products of the vascular strands within, and consequently must wither, and ultimately be thrown off. So that in an older root, in one where secondary xylem and phloem have been formed, there is no trace of an endodermis, cortex, or piliferous layer, these having been thrown off by the development of many layers of cork cells. Hence an old root cannot be absorptive: in fact we

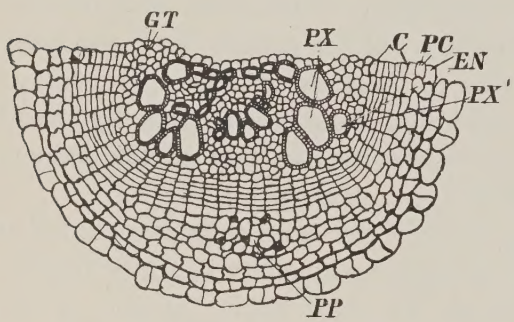


FIG. 44. One half of a transverse section of the root of Sunflower (*Helianthus annuus*), taken through the region of the lateral roots, but avoiding them. C = cambium; EN = endodermis; GT = intra-stelar tissue (ground-tissue); PC = pericycle; PP = primary phloem; PX = primary xylem; PX' = protoxylem.

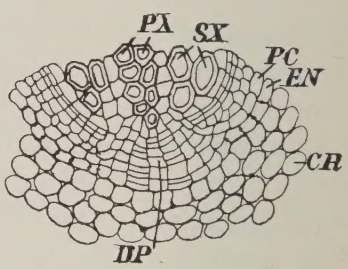


FIG. 45. A small portion of a transverse section of the root of Pea (*Pisum sativus*) to show the division of some of the pericycle and endodermal cells as the first stage in the development of a lateral root. CR = cortex; DP = dividing (merismatic) cells of pericycle and endodermis; EN = endodermis; PC = pericycle; PX = primary xylem; SX = secondary xylem.

may say that the older parts fix the plant to the soil; the piliferous portions (hair-bearing portions) are absorptive; the apical portion in front of these is the growing part; and the root, as a whole, is a conducting channel, conveying the water and dissolved mineral matter through its xylem strands to those of the stem, thence to the leaves.

Development of lateral roots. Lateral roots, unlike shoots and leaves, arise **endogenously**—that is, from the central tissues. A lateral root arises from the pericycle and endodermis opposite each primary xylem group (Fig. 45), and since there are usually four of these, the arrangement of the lateral roots in four strands, as already described, is thus explained. The first indication of the development of the lateral root is a radial elongation of the pericyclic and endodermal cells (Fig. 45, DP), as a result of which they encroach

upon the cortex. These elongated cells then divide by tangential (periclinal) walls, and constitute what will later become the apex of the root. By the continual division of the mass of cells thus formed, the rootlet gradually grows outwards, the cells at its apex absorbing the cortical cells as the rootlet advances. This mass of cells permanently retains the power of division, and so can form new tissue continually; careful examination of the apex of a developing lateral rootlet (Fig. 46)

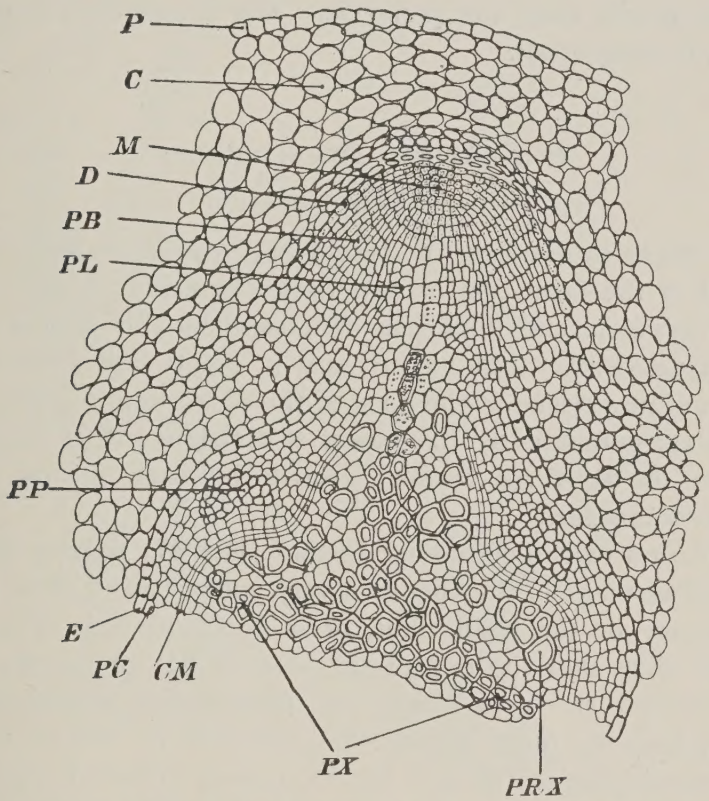


FIG. 46. A portion of a transverse section of the root of Pea (*Pisum sativus*), showing the later stages in development of a lateral root. C=cortex; CM=cambium; D=dermatogen; E=endodermis; M=apical meristem; P=piliferous layer; PB=periblem; PC=pericycle; PL=plerome; PP=primary phloem; PRX=secondary xylem; PX=primary xylem.

will show that from this undifferentiated mass of tissue, called the **apical meristem** (M), the central cylinder (PL), the cortex (PB), and the piliferous layer of the lateral root are derived, as well as the root-cap at a slightly later stage. And it further shows (Fig. 46) that the vascular bundles, endodermis, cortex, and other parts are continuous with the corresponding portions in the parent root. (See also Apical Development, infra, pp. 72–6.)

(*b.*) Root of Sunflower.

In respect of nearly every detail, the root of the sunflower is the same as that of the bean-plant. It differs from it, however, in the structure of the apex, a feature that will be studied later, and in the mode of origin of the lateral roots. In the bean-plant the lateral roots arise from the pericycle, endodermis, and, to a very small extent, from the cortex. But in the sunflower and in phanerogams generally they arise wholly from the pericycle. The endodermal origin, as in the bean, is exceptional.

(E.) Apical Development.

(*a.*) The Shoot.

The increase in diameter of a dicotyledonous shoot takes place as the result of the formation of new tissue, by means of the cambium ring; increase in the thickness of a stem by this means is called **secondary growth.** But its increase in length takes place by the formation of new tissue at the apex of the stem, from a group of cells which retain permanently the power of division, and is hence called **meristem** or **dividing tissue**; growth by such means is called **apical development.**

Examination of a longitudinal section (Fig. 47) passing accurately in the median plane of the apex of a very young lateral shoot of either the sunflower or the bean-plant, or of the main axis of a seedling plant, will show that the end of the stem is flat, or slightly convex; a little behind the apex there are papillæ-like elevations, which become larger the more distant they are from it. These elevations are the developing leaves and shoots, closely crowded together, the very youngest (smallest) nearest the apex, the oldest (largest) farthest from it; they thus develop in acropetal succession.

The apex and the lateral outgrowths are limited externally by a single layer of cells (D), which are continually dividing by the formation of new cell-walls at right angles to the surface (**anticlinal walls**), but which never divide by walls parallel to the surface (**periclinal walls**). Traced backwards, this formative layer is found to be continuous with the epidermis, and obviously is the layer from which the epidermis, both of the stem and the leaf, is derived; it is, therefore, called the **dermatogen.** Some of its cells (H) grow outwards as papillæ-like elevations, which divide several times; these will form the

multicellular hairs, which are, therefore, emergencies derived from the dermatogen. Beneath the dermatogen at the apex, there is an undifferentiated mass of cells (A.M), with thin walls, large nuclei, and rich in protoplasm, vacuoles being absent. From this portion of the meristem (the dermatogen is the other portion) are derived two strands of tissue: an inner central one, the **plerome** (PL), and an outer one, situated between the plerome and the dermatogen, the

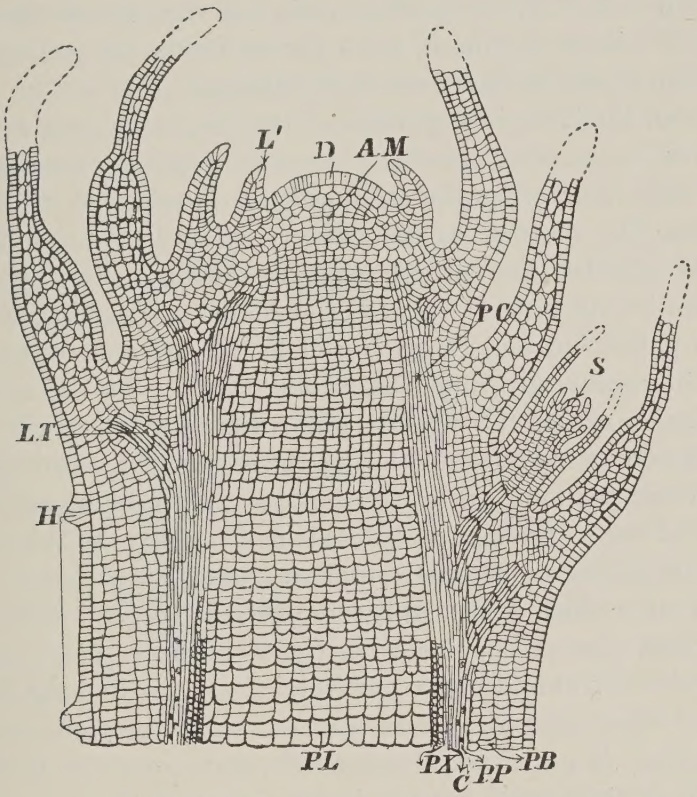


FIG. 47. Median longitudinal section through the apex of the stem of Sunflower (*Helianthus annuus*). A.M = apical meristem; C = cambium; D = dermatogen; H = developing hairs; L′ = developing leaf; L.T = leaf-trace; PB = periblem; PC = procambium; PL = plerome; PP = protophloem; PX = protoxylem; S = developing shoot (bud).

periblem (PB); the former gives origin to the tissues composing the pith and vascular bundles, including the pericycle, and the latter to the whole of the cortical tissues.

In most plants and in favourable sections, the meristem may be clearly distinguished into three layers: an outer dermatogen; beneath this a single layer of cells, the periblem, which farther back becomes two or three layers thick; and beneath this, a group of cells, dividing in all directions, the plerome. But this is not the case in the sun-

flower, where the periblem and plerome are not distinct from one another at the apex, but arise from a group of cells common to both.

The cells of the dermatogen divide by anticlinal walls only; those of the periblem by both anticlinal and periclinal walls; while those of the plerome divide in all directions, except certain strands of cells upon the outside of the plerome, which divide more frequently by longitudinal than by transverse walls, so that these cells are much longer than wide. These tracts of cells are the **procambial strands** (PC), and the inner portion of each strand forms the **primary xylem** and the outer portion the **primary phloem**. During the elongation of the shoot the innermost portion of the primary xylem lignifies and forms spiral and annular vessels; these constitute the **protoxylem** (PX). It is not until later, when the region of the shoot involved has ceased to elongate, that the rest of the primary xylem becomes differentiated and forms lignified and pitted vessels. Owing to the fact that the protoxylem is thus differentiated in the elongating portion of the stem, it is often pulled out and disorganized by the stresses set up within it, through the rapidly growing tissues investing it. In the same way as in the primary xylem, the primary phloem is also differentiated into an earlier formed **protophloem** during the elongation of the shoot, and a later formed portion; but in the phloem the protophloem lies to the outside, and not to the central side as in the xylem. Thus each procambial strand begins its differentiation at two points, which lie at the inner and outer sides respectively; the protoxylem is differentiated at its inner and the protophloem at its outer limit. Each procambial strand is also surrounded by a small-celled zone, called the **peridesm**, the cells of which also pass in between the primary xylem and phloem. The peridesm is potentially merismatic, and gives rise later, on the inner limit of the strand (to the inner surface of the protoxylem) to a strand of small-celled tissue, the **perimedullary zone**; on the outside to the **pericycle** and pericycle fibres; between the procambial strands to the **primary medullary rays**; and between the xylem and phloem to the **cambium**.

The first indication of the **development of a leaf** (L′) is the more rapid division of certain cells of the periblem beneath the dermatogen; these divide at first by periclinal walls, and thus bulge the dermatogen outwards, but later they divide as well by anticlinal walls. By thus continually dividing the outgrowth becomes bigger, but still only consists of the covering dermatogen which becomes the epidermis of the leaf, and a central mass of parenchymatous cells, which forms

the central tissues of the leaf. The cells at the base retain the power of dividing for a long time, while those within the leaf soon lose this power. At a comparatively early stage in the development of the leaf, certain of the central cells elongate and give rise to the vascular bundle, which gradually extends inwards towards the stem, and ultimately meets and merges with a vascular outgrowth (L.T) of the bundle of the stem. The whole of the leaf, including its bundle, is thus developed from the superficial layers of the periblem, the plerome taking no share whatever in the process. The same holds true of the **development of a shoot** (Fig. 47, S), which only differs from the leaf in that deeper layers of the periblem take part in its formation, and in that it arises in the axil of a leaf.

Leaves and shoots are **exogenous** in development—that is, they are derived from superficial and not central tissues. This is one of the most constant differences between a shoot and a root, the latter of which **is endogenous** (cp. supra, p. 70).

(*b.*) The Root.

(*a.*) The Sunflower Root.

The root forms no leaves and so never develops buds, but unlike the stem it forms a root-cap at its apex, hence its apical development will exhibit certain differences from that of the stem. Examination of a perfectly median section of the apex of a root (Fig. 48) will show that the growing point (AP) is not at the extreme apex, as in the stem, but some little way behind. The geometric apex of the root is occupied by a mass of cells (RC), the inner ones of which are actively dividing ; this is the **root-cap** or **calyptra.** Traced inwards to the growing point of the apex (AP) (*punctum vegetationis*), it is found to arise from the outer one (CY) of two layers, by periclinal divisions of its cells. If these two layers be traced backwards to beyond the boundaries of the root-cap, they will be found to be continuous with the piliferous layer of the root, which is derived from the inner layer of the two by anticlinal divisions of its cells. Thus the outer layer gives origin to the root-cap and may be called the **calyptrogen**, and the inner to the piliferous layer, which may therefore be named the dermatogen. Beneath the dermatogen (D) is a single layer (P) of merismatic cells, which farther back become several layers thick ; the tissue derived from this initial group is the **periblem**, and like that in the stem it gives origin to the cortex, including the endodermis, of the root

Beneath this is a group of cells (PL), from which the **plerome** is derived, and that in its turn gives rise to the central vascular cylinder, including the pericycle of the root.

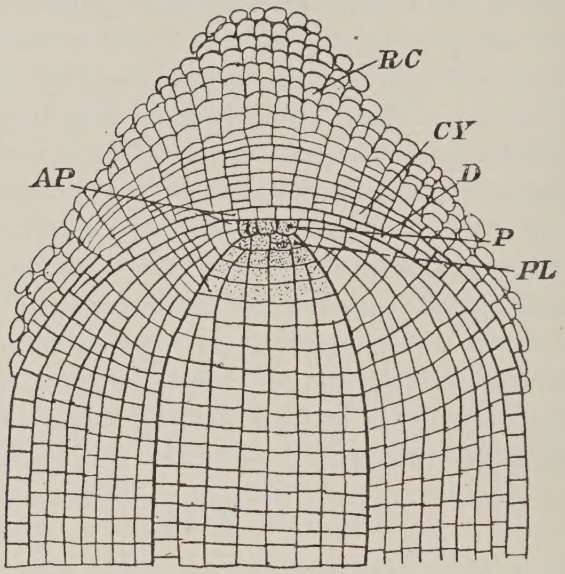


FIG. 48. Median longitudinal section through the apex of the root of Sunflower (*Helianthus annuus*). AP = apical meristem; CY = calyptrogen; D = dermatogen; P = the layer of merismatic cells which gives rise to the periblem; PL = the merismatic cells which give rise to the plerome; RC = root-cap.

We see that in the sunflower, the tissues of the root are derived from three layers which are quite distinct one from another at the apex: i. e. the calyptrogen and dermatogen, periblem, and plerome.

(β.) THE BEAN-PLANT ROOT.

At the apex of the bean-plant root (Fig. 46), the meristem is not thus divided into three distinct layers, but is an undifferentiated mass of cells (M), from which the plerome (PL), periblem (PB), dermatogen (D), and calyptrogen are derived. In other words, if the tissues of the root be traced upwards, they will converge not to three distinct layers, but to an undifferentiated group of dividing cells.

There are thus in roots two types of meristem: the one differentiated into three layers, to which the sunflower and most dicotyledons belong, and the other undifferentiated, to which the bean-plant and a few other dicotyledons belong.

In both roots, the root-hairs arise as filamentous outgrowths of the cells of the piliferous layer, and remain unicellular throughout life.

CHAPTER III

ARBOREOUS PLANTS

THE ELM (*Ulmus*).

1. External Characters.

(A.) The Shoot and Root.

In Britain two species of elm are to be found, the common elm (*Ulmus campestris*) and the wych or mountain elm (*Ulmus montana*). By some botanists these two species are regarded as merely varieties or races of one species, since the differences which separate them are more or less bridged over by structural variations in both. The common elm is a tree of considerable size and massive proportions, the main axis or stem being wide at the base and gradually tapering to a filament at its apex. This elongated conical form of the stem is characteristic of dicotyledonous and gymnospermous trees and contrasts with that of monocotyledonous ones, which are of uniform diameter throughout their length; this difference is one which is correlated with the fact, that in the latter class of trees, the stem when once formed is not thickened by the addition of fresh tissues internally, so that it grows in length—by growth at its apex—without increasing in diameter. In dicotyledons and gymnosperms, the stem is increased in thickness every year by the addition of fresh tissues as the result of the activity of the cambium ring, and it follows therefore that the older the part of the stem, the thicker it will be, since more tissue has been added to it than in the younger parts; and as increase in length takes place at the apex, this will be the youngest part and the base the oldest, hence the elongated conical form assumed by all trees in which secondary thickening, by the addition of annual cylinders of tissues, takes place.

The stem branches profusely, and the main axis is a very obvious one; the largest of the lateral branches are the lower ones, and gradually they get smaller towards the apex of the main axis. The mode of branching therefore is a monopody (supra, p. 6). Not infrequently, however, it tends to become a false dichotomy, especially with the lower branches, when one or more of the lateral branches

grows nearly as vigorously as the main stem, so that there is apparently a forked main axis.

The leaves are egg-shaped (ovate) and each leaf is attached to the branch by a short stalk or petiole (petiolate). A characteristic feature in the form of the leaf is its asymmetry, one half being longer towards its base than the other. The margin is broken up by a number of saw-like teeth (serrate), each tooth really consisting of two (bi-serrate); the under surface is downy and the upper rough with rough hairs. The leaves are **deciduous**, that is, they fall off in the autumn, and fresh ones are formed in the following spring. The shoots arise in the axils of the leaves of the current year, in the form of small buds (Fig. 49, B), which are protected by brown scale leaves (SL), and persist throughout the winter. In the following spring each bud unfolds, the scale leaves drop off, and the axis of the bud elongating, carries its leaves wider apart, so that by degrees the bud becomes a well-developed shoot, consisting of a stem and leaves. During the greater part of the first year the stems of these young shoots remain green, but at the end of autumn they become covered with a thin layer of cork, similar to that investing the older twigs, and assume a brown colour in consequence.

The root penetrates to great depths in the ground, and spreads laterally to a considerable distance. It is a tap-root, and like the stem branches monopodially. With the exception of the terminal rootlets, which are the absorptive parts of the root, the root-branches are invested in a protective corky layer.

(B.) The Flower and Fruit.

The flowers are borne in reddish clusters (Fig. 49, F) in the axils of leaves of the previous year, and are developed before the leaf-buds of the current year are unfolded. At first the flowers are invested within, and thus protected by brown membranous bud scales (SL), which soon fall off. The perianth (Fig. 49, II, P) is broadly bell-shaped (campanulate), and consists of a variable number (4 to 6) of lobes, which are brown and membranous in appearance, the base of the perianth being green. The stamens (S) are equal in number to the lobes of the perianth, and are attached by long filaments to the floral receptacle opposite each lobe. The gynæcium (G) is bicarpellary and bilocular, flattened and green in colour. The styles, like the gynæcium, are flattened and are two in number, becoming divergent as

the fruit forms; the stigma (SG) is situated on the inner surface at the extremity of each style, and is hairy in texture and brown in colour.

The flowers are not conspicuous, and are devoid of those pleasing colours and sweet smelling odours that we usually associate with the idea of flowers, and neither are there any nectaries present. The absence of these qualities renders the flowers unattractive to insects, so that they depend entirely upon wind and gravitation for their pollination (infra, p. 306). The flowers are hermaphrodite (both stamens and carpels in each flower), so that self-pollination is rendered possible, and, indeed, in this particular case, almost inevitable from the relative position of the stamens and carpels and their simultaneous attainment of maturity. In a great many hermaphrodite flowers (infra, p. 308) various devices, including the ripening of the stamens before the carpels or vice versa, are adapted to prevent self-pollination, but in the elm this is not the case. In nearly all wind-pollinated flowers, the stigma is relatively large, expanded and hairy, thus increasing the chances of pollination being effected, but in the elm flower the stigma is not characterized by any of these qualities. This difference is probably correlated with the fact that most of the wind-pollinated flowers are unisexual, so that the pollen has to travel through the air from one flower to another, and in some cases from one plant to another; whereas the elm flower is capable of self-pollination, so that in the former case it is necessary to reduce the chances of failure of pollination as far as possible, while in the latter case, if pollination by the pollen from another flower fails to take place, there is always self-pollination to fall back upon.

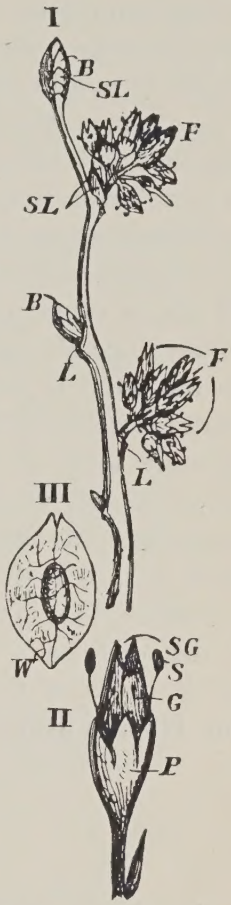


FIG. 49. I. A twig of the previous year of the Wych Elm (*Ulmus montana*). II. A single flower, enlarged two and a half times. III. A single fruit (samara), enlarged one and a half times. B = bud. The lowest bud on the twig is aborted. F = cluster of flowers; G = gynæcium; L = leaf-scars of the previous year's leaves; P = perianth; S = stamen; SG = stigma; SL = scale leaves; W = membranous expansion or 'wing' of fruit.

As already indicated, the gynæcium is bilocular (divided into two compartments), and in each compartment there is a single ovule

suspended from its upper wall. After fertilization (infra, p. 136), the gynæcium ripens into the fruit, and the ovules into the seeds. During the maturation of the gynæcium, a membranous structure grows outwards from all round the margin of it and forms an annular wing-like expansion, while internally one of the two compartments (loculi) together with its contained ovule becomes suppressed. The ripe fruit is therefore a winged, one-seeded capsule, which is known under the technical name of **samara** (infra, p. 318). The presence of the membranous annular wing adapts the fruit to be conveyed by currents of air to some more or less considerable distance from the parent plant, since the weight of the wing compared to the surface exposed to the wind is very little. The young seedlings are thus enabled to germinate and to continue their growth under conditions where there is more light, air, and nutriment than would be obtainable were the fruits to fall vertically downwards from the parent plant, and to germinate directly beneath it. The development of the wing upon the fruit is thus a device for minimizing the results of the struggle for existence, that is the inevitable lot and the ever-pressing need of every living organism. A similar device is seen in other cases, such as that of the fruits of the maple and ash, and the seeds of the pines (infra, pp. 145 and 319).

2. Internal Structure.

(A.) The Stem.

As already indicated, the arboreous stem passes through a herbaceous stage, when a bud develops into a twig of the current year's growth. Examination of a transverse section through the herbaceous twig of the current year's growth will show that, in its principal features, it resembles the young sunflower stem. Externally it is limited by a single-layered epidermis (Fig. 50, E), composed of oblong cells, the outer walls of which are thickened and cuticularized. Many of the epidermal cells grow out in the form of unicellular, conical hairs, in the walls of which silica is deposited; if a section containing such hairs is treated with potassium chlorate and nitric acid, and warmed, all the organic portion of the hairs and section is dissolved, but complete skeletons moulded in silica are left behind, which resist the action of the liberated chlorine. Stomata are present in the epidermis. Within the epidermis are several layers of cortical parenchyma (C), composed of cells with cellulose walls, containing chloro-

phyll, and with intercellular spaces between them. Here and there are cells with much swollen walls, often to such an extent that the cavity of the cell becomes obliterated; these are mucilaginous cells, so called, because their walls are converted into mucilage, a substance that swells enormously in the presence of moisture.

At the basal portion of the herbaceous twig, there is developed between the cortex and the epidermis (Fig. 50, CR) several layers of cork cells. These arise by the division of the cortical cells lying just beneath the epidermis, by thin periclinal walls; a **cork cambium** or **phellogen** (P) is thus formed, and this divides off cells to its outside, the walls of which become suberized and the protoplasm used up; these are the cork cells (CR). The cork is not developed in the younger part of the twig until towards the end of the autumn.

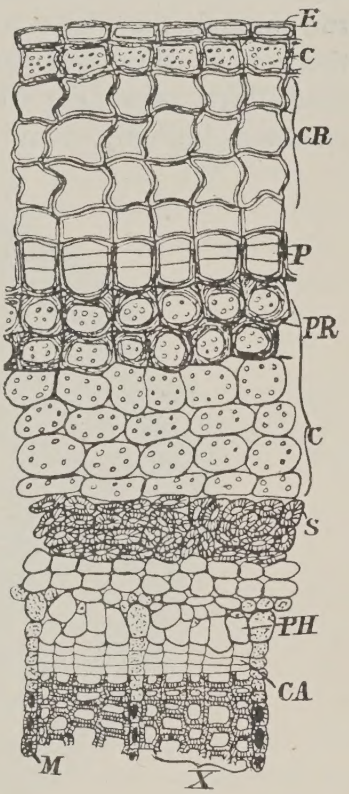


FIG. 50. A small portion of a transverse section through the stem of the current year of Elm (*Ulmus campestris*). Only the outer portion of the xylem is represented. C = cortex; CA = cambium; CR = cork cells; E = epidermis; M = medullary ray; P = phellogen or cork cambium; PH = phloem; PR = phelloderm, composed of collenchyma; S = sclerenchyma (pericycle); X = secondary xylem.

Scattered about in the pericycle within the cortical tissue, and forming a more or less regular ring, are patches or strands of sclerenchyma (S), the fibres of which are very thick-walled. Many of these strands lie immediately without a vascular bundle, but they are not so definitely related to them as in the sunflower. The pericycle is thus heterogeneous.

The vascular bundles are not independent of each other, that is, they form a more or less continuous ring, but consist of the same elements as those in the sunflower. The phloem (Fig. 50, PH) is composed of sieve-tubes and phloem parenchyma, but companion cells are absent. The cambium (CA) is similar to that in the sunflower, but it is more active and consists of a larger number of cells radially arranged. The xylem (X) forms a broad band of lignified tissue and is composed of vessels, fibres, and xylem parenchyma, not so regularly arranged as those in the sunflower. The details

of the xylem will be studied in an older stem. The inner margin of the xylem band is crenated, the crenations being formed by the projections of the apices of the protoxylem wedges into the pith, which project into it beyond the inner margin of the secondary fascicular and inter-fascicular xylem. The inter-fascicular xylem is separated from the fascicular wedges by medullary rays (M), which run through the whole width of the vascular ring, from the pith to the cortex; these are the **primary medullary rays**. **Secondary medullary rays** (Fig. 51) are mostly formed by the inter-fascicular cambium, but only extend part of the way through the xylem, and part

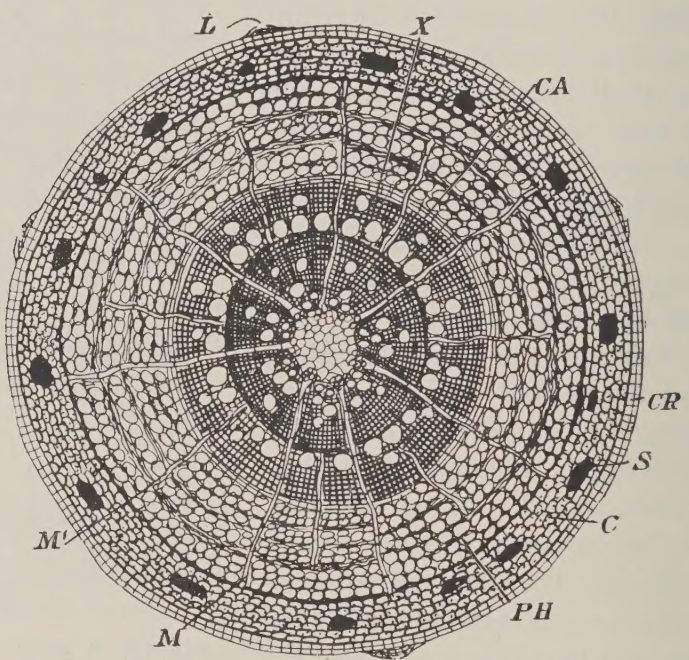


FIG. 51. Transverse section of a two-year-old twig of Elm (*Ulmus campestris*). Magnified about 80 times. C=cortex; CA=cambium; CR=cork; L=lenticel; M=primary medullary ray; M'=secondary medullary ray; PH=phloem; S=strand of sclerenchyma; X=xylem. The larger spaces in the xylem are those of the xylem vessels, and the others those of the xylem fibres and parenchyma. The xylem contains two annual rings.

of the way to the periphery in the phloem, so that in the former they do not reach the pith and in the latter they do not extend to the cortex.

We thus see that the herbaceous twig of the elm differs from the younger part of the sunflower stem, in that the bundles have become merged by the formation of inter-fascicular xylem and phloem and form a vascular ring. But a section taken through the apex of the twig, i. e. through the terminal bud, will show that the bundles are distinct; in arboreous stems, however, the inter-fascicular cambium is very

early developed, and as a consequence, that condition which is only reached in the older portions of the sunflower stem and then late in the year, is very early developed in arboreous twigs.

Examination of a section of an older twig (Fig. 51) two to four years old, will show the same general arrangement as that just described, but the increase of the secondary xylem (X) and phloem (PH) has been relatively great, and the cork layers (CR) have been very much increased. The epidermis is withered and is no longer recognizable, while the cork now forms several layers of regularly arranged thin-walled cells. At intervals along the section, the surface of the cork projects outwards, and it will be seen that here the corky layer is very much thicker than elsewhere, forming a more or less semi-circular mass of cork cells (Fig. 51, L), which differ from the ordinary cork cells, in that there are intercellular spaces between them. This mass of cells (Figs. 51 and 52) is a **lenticel**, and if the section has passed accurately in the median plane through it, it will be seen that it opens to the exterior by an aperture (S); this latter is often the persistent stoma of the epidermis of the herbaceous twig, but in older portions, they are formed independently of stomata. The lenticels are breathing and nutritive organs, allowing the oxygen and CO_2 of the atmosphere to gain access to the chlorophyll-containing cortical parenchyma.

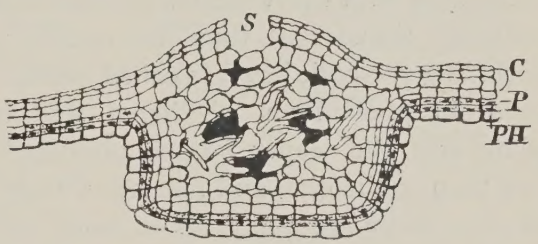


FIG. 52. A lenticel of the stem of Elm (*Ulmus campestris*). Magnified 300 times. C = cork cells; P = phellogen or cork cambium; PH = phelloderm; S = stoma or external aperture of lenticel.

To the inside of the cork-layer is the **phellogen** (Figs. 50 and 53, P), or **cork cambium**, composed of a single layer of narrow, very thin-walled cells, with plentiful protoplasm. To the inside of this are several layers of thick-walled cells, with chlorophyll grains; this is the **phelloderm** (P′), and like the cork cells has been derived from the phellogen, the former being the daughter-cells given off to the inside, and the latter those given off to the outside of it. Beneath the lenticels, the phellogen and phelloderm curve round them (Fig. 52), and intercellular spaces occur in both tissues, so that the similar spaces of the cortical parenchyma are thus placed in connexion with those of the lenticels, and thence with the exterior.

A free interchange of gases can thus take place, between the chlorophyll-containing cortex and the atmosphere.

We have already seen that the phellogen is derived by the formation of periclinal walls in the cortical cells lying just beneath the epidermis (Fig. 50). But as the stem grows older, the phellogen is formed at successively deeper positions, so that in old stems, in those for instance in which the bark is not smooth but fissured, it will be found that there are one or two corky layers extending round the stem in the secondary phloem; these deeply-seated corky layers are derived from a phellogen that arises from the phloem parenchyma, in the same way that the more superficial phellogen arises from the cells of the cortical parenchyma. As a result of this deep-seated formation of phellogen, some of the phloem, i. e. all that to the outer side of the phellogen, and all of the cortex, become cut off from physiological connexion with the vascular strands, and so die and wither. All the withered tissue that thus lies outside the innermost band of cork, including the cork itself, is called **bark**. The **periderm** is the whole mass of phelloderm, phellogen, and bark. In the vine and the plane-tree, the deeper formed phellogen is formed at a much earlier age than in the elm, and instead of there being but one or two bands of cork, there are many, six or more, according to age.

Within the periderm is the cortical parenchyma (Fig. 53), but compared to the bulk of the vascular tissues, it is insignificant; it is of the same nature as that already described for the younger twig, though the sclerenchyma strands (S) and mucilage cells are more abundant. Idioblasts (cells with large crystals) are also more plentiful than in the twig of the current year. Many of its cells are also dividing by radial walls, so as to keep pace with the secondary growth of xylem and phloem.

The phloem (Fig. 51, PH) is a much thicker layer than that in the younger stem, though it is much narrower than the xylem; it is more or less distinctly marked off into concentric rings, the number of which have some relation to the age of the stem, though not the same constant numerical relation that those of the xylem have. The bands of phloem are frequently interrupted by the passage through them, entirely or partially, of the medullary rays (M), which while traversing the phloem have thin cellulose-walled cells. In older stems, about six to seven years and more, some of the phloem and phloem parenchyma become crushed (Fig. 55) as the result of the increase in the secondary xylem within and the presence of the

inelastic and unyielding cork without; the phloem becomes squeezed as in a vice.

The phloem passes gradually into the cambium (Figs. 51 and 53, CA), the as yet unaltered daughter-cells of which are very much more numerous than in the case of the sunflower stem or the twig of the current year. Careful examination of it shows that the actual cambium is but a single layer, and that the cells of which it is composed divide according to the law of Sanio (supra, p. 50).

Within the cambium is the xylem (X), which in all arboreous stems forms much the greater portion of the bulk of the stem. It is composed of vessels, fibres, and xylem parenchyma, and is traversed by primary and secondary medullary rays. The xylem vessels are principally of the following kinds: **spiral vessels** (Fig. 53, SV), belonging to the protoxylem, and situated in groups at the central part of the xylem, abutting upon the pith; **pitted vessels** (PV), with bordered pits and having larger cavities than any of the others; **pitted-reticulate vessels** (Fig. 23, IV), occurring in groups and having small cavities.

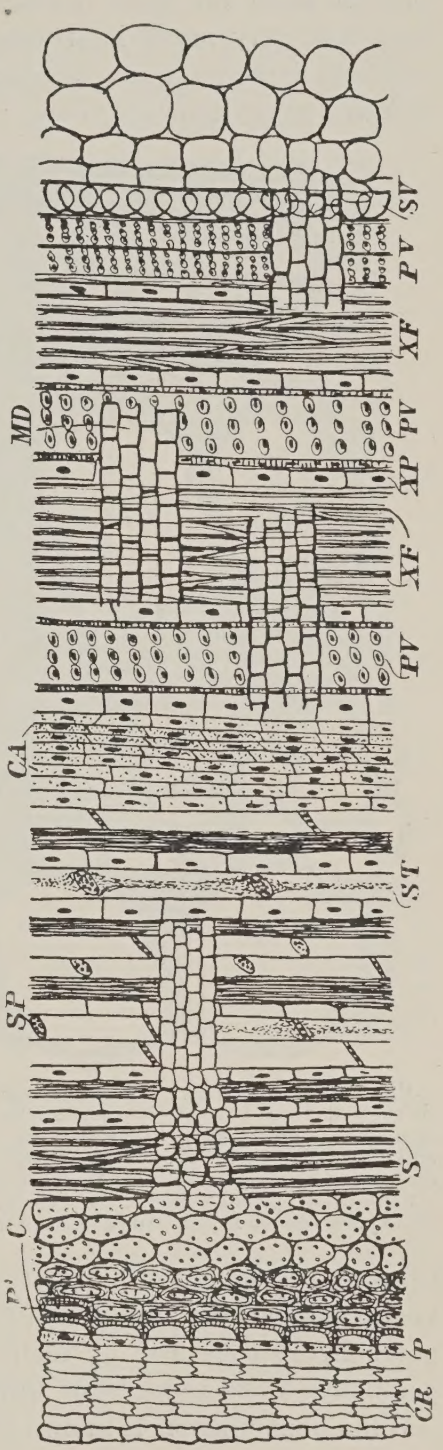


FIG. 53. Radial longitudinal section of stem of Elm (*Ulmus campestris*). Magnified 300 times. C = cortex; CA = cambium; CR = cork cells; MD = medullary ray; P = phellogen or cork cambium; P′ = phelloderm; PV = bordered-pitted vessel; S = sclerenchyma (differentiated portion of pericycle); SP = sieve-plate; ST = sieve-tube; SV = spiral vessel of protoxylem; XF = xylem fibres; XP = xylem parenchyma. The parenchymatous tissue to the extreme right of the section is that of the medulla or pith.

In these last vessels both bordered pits and reticulate markings are present upon the same walls. The xylem fibres (Fig. 53, XF) are long and very much intertwined, so that in a longitudinal section, which is limited to a mathematical plane, an individual fibre is seldom followed along its whole course; they have no cell contents and their walls are pitted. The xylem parenchyma (Figs. 53 and 54, XP) is composed of oblong and squarish cells with protoplasmic cell contents and starch, and thick, lignified, simple-pitted walls; they occur in longitudinal bands, and usually more or less completely surround the vessels, and come into contact with the medullary rays; frequently they are arranged in tangentially disposed bands placing one medullary ray in connexion with another. Not infrequently a cell of the parenchyma which surrounds the xylem vessels grows through the pits in the wall, pushing the pit-membrane before it, and enters the cavity of the vessel. In Fig. 57 there is represented at A a little papilla-like bud derived from the parenchyma cell P, lying just outside the vessel; at B there is represented one at a little later stage, after it has grown well into the cavity of the vessel. At C, the cavity of the vessel has become almost obliterated by the invasion of several such parenchyma cells and by their subsequent division. The mass of parenchymatous tissue thus formed within a vessel is called **tullen**, and the phenomenon is known as **thyloses**. Its meaning is not very

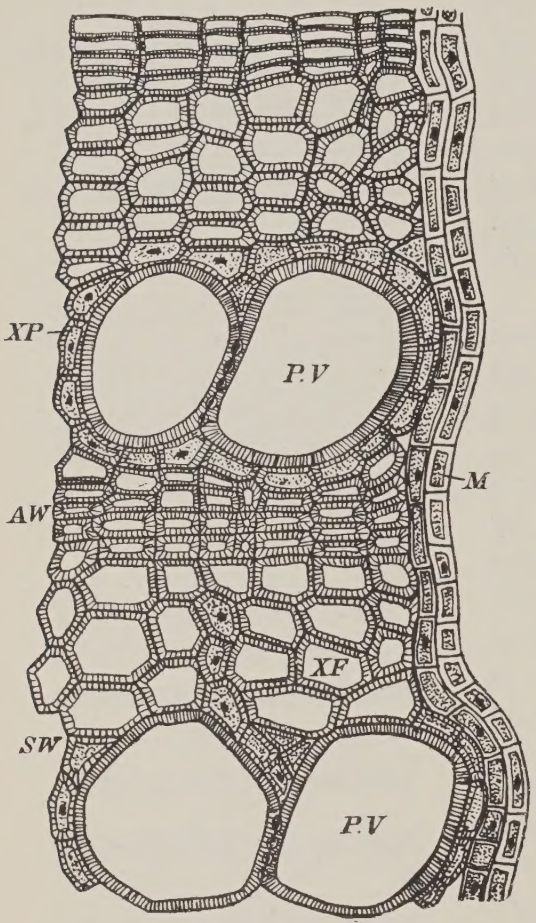


FIG. 54. A portion of a transverse section through the wood or xylem of the Elm (*Ulmus campestris*), including a part of two annual rings and a medullary ray. Magnified 300 times. AW = autumn or later-formed wood; M = medullary ray; P.V = bordered-pitted vessels; SW = spring wood; XF = xylem fibres; XP = xylem parenchyma.

clear, but it is of common occurrence in the xylem of arboreous stems, and can usually be seen in sections of elm stem or of the so-called acacia (*Robinia Pseud-acacia*).

The medullary rays (Fig. 54, M), while traversing the xylem, possess the same characters as the xylem parenchyma; each ray is composed of two layers of cells, arranged in several tiers (Figs. 53 and 55), so that, structurally considered, they are not unlike brick walls traversing the xylem. The primary medullary rays pass right through the phloem and the xylem, from the cortex to the pith, while the secondary ones stop short, farther or nearer to the pith on the one side and the cortex on the other, according to their age.

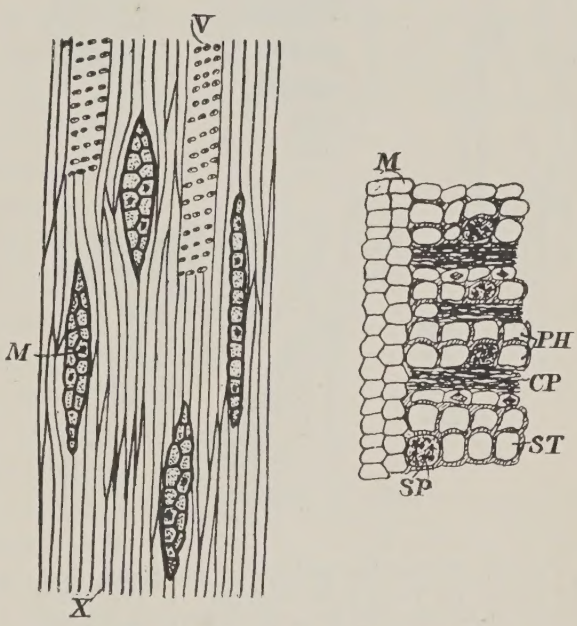


FIG. 55. The right-hand figure represents a transverse section through the phloem of a seven-year-old stem of the Elm. CP = crushed phloem; M = medullary ray; PH = phloem; SP = sieve-plate; ST = sieve-tube. The left-hand figure represents a tangential longitudinal section through the xylem of the Elm, and showing the cut ends of the medullary rays (M); V = vessel; X = xylem fibres.

A superficial examination of the xylem will show that it is composed of a number of concentric rings – four if it is a four-year-old stem and three if a three-year-old stem. These rings are **the annual rings**, so called because they are formed one in each year. The cambium during the spring, summer, and early part of autumn is continually forming both secondary xylem and phloem, but in late autumn and winter its activity ceases and it remains dormant until the next spring, when it forms more xylem and phloem. Thus every ring is the product of continuously deposited xylem, and the junction between every two rings the expression of a break in the continuity of formation. Careful examination (Fig. 54) of any one ring will show that it is not constituted alike throughout its width: that which forms its inner portion is formed in the spring of the year, and is composed mainly of vessels (P.V), many of which have large cavities, with a few fibres; while that

which forms its outer portion and is formed in the late summer or early autumn of the year, is composed almost wholly of fibres (XF), of thicker walls and smaller cavities than those formed in the spring or summer. Hence each annual ring consists of spring (Fig. 54, SW) and autumn[1] (AW) wood, with their own characteristics, with the summer wood between them and not particularly distinguished by any characters of its own. In an arrangement of concentric rings thus constituted, it follows that the autumn wood of denser texture of the preceding year will directly abut upon the spring wood of large vessels of the succeeding year; it is this sharp contrast of xylem thus differently constituted that marks the limits of each annual ring, and produces the optical expression of concentric lines upon a tree trunk cut across the surface and smoothed.

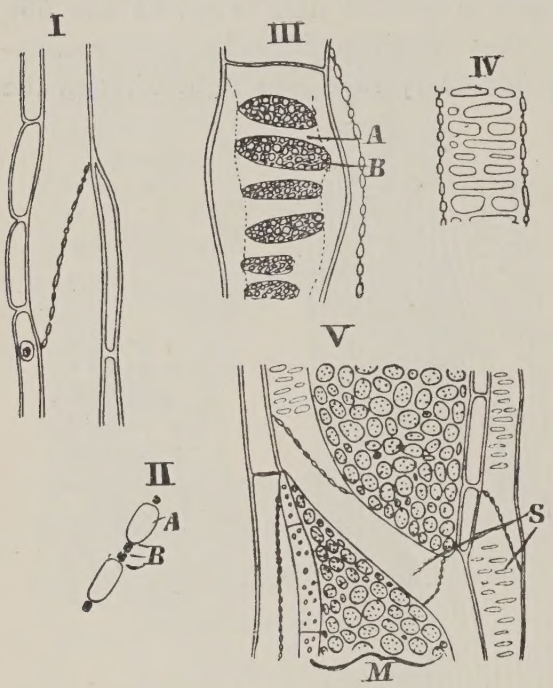


FIG. 56. Sieve-tubes with compound plates, from the stem of the Vine (*Vitis vinifera*). I. Tangential section of a sieve-tube and companion cells, showing a compound sieve-plate in section. II. A small portion of the sieve-plate in I, more highly magnified (about 300 times). A=the thickening of the plate; B=pores (see p. 43). III. Radial section (at right angles to that represented in I) of a sieve-tube, showing numerous sieve-plates on a transverse wall which is highly inclined, and the form of which is indicated by the dotted lines. A=thickening; B=pores. IV. Sieve-plates in surface view and in section on the vertical walls of a sieve-tube. V. Tangential section passing through a medullary ray and the phloem portions of two bundles, showing a sieve-tube connexion between the latter. M=medullary ray; S=sieve-tube.

Many explanations have been put forward as to the causes operating in the production of different kinds of wood at different seasons of the year; of these, we need alone concern ourselves with two. In the spring of the year, when the leaves have opened from the bud, the plant is very active, and it is taking up by its roots and giving off from its leaves a greater

[1] Some authorities object to the term *autumn* wood and prefer that of *later* wood, because it is doubtful whether the cambium is very active in the autumn, and consequently whether any wood is formed at that period.

quantity of water than it will at any other season; the channel by which the water passes from the roots to the leaves is the xylem, and hence there passes through it much more water in the spring than in the summer or autumn. And it is thought that the production of the larger cavity vessels and fibres at this season of the year is correlated with the larger amount of water passing through them, while they are as yet in the plastic state and not completely lignified. On the other hand, it is contended that since the stem is encompassed without by a more or less inelastic and unyielding bark, the xylem is formed in the late summer and autumn under a greater pressure than that in the spring, since the wood formed in the spring and early summer has increased the pressure upon the internal tissues in virtue of the additional thickness thus added.

Neither of these explanations, either singly or combined, explains the known facts; such as, for instance, that in many trees the annual rings are the same throughout—there is no distinction into spring and autumn wood. But, nevertheless, they contain some germ of truth, for there can be but little doubt that the greater ascent of water in spring and the increase of pressure upon internal tissues as the year advances must exercise some influence upon developing tissues.

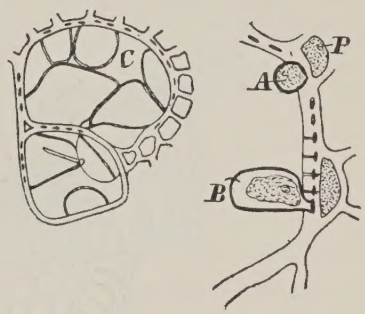


FIG. 57. Thyloses in the xylem of *Robinia Pseud-acacia*. A=papilla-like bud of a parenchyma cell protruding through a pit into the cavity of a xylem vessel; B=a more advanced papilla; C=a parenchymatous tissue called tullen filling the cavity of a xylem vessel; P=a cell of xylem parenchyma.

Within the ring of xylem and centrally of all is the pith (Fig. 51). Peripherally it consists of cells, with thick, lignified, pitted walls, protoplasmic contents and starch. Centrally the cell-walls are lignified and pitted, but much thinner, and the cells contain no protoplasm.

We thus see that at a very early stage, while yet in the bud condition, the arboreous stem is fundamentally like the herbaceous stem of the sunflower, and the vascular bundles are separate from one another; but in older portions of the current year's twig the vascular bundles become united and form a ring, by the development of interfascicular cambium, phloem, and xylem, just as in older portions of the sunflower stem; and in the same manner that cork may be formed at the basal portion of this latter stem in the autumn, so in

the current year's twig of the arboreous stem cork is developed. And, moreover, the seedling elm passes through this herbaceous stage. But it is at this stage that the sunflower stops in its progress, for the simple reason that it dies at the end of the season after the fruit has ripened; while that of the elm remains dormant through the winter and in the following spring renews its activity, so that by the end of the year another ring of xylem, phloem, and cork has been added to that already existing. This is continued year after year, and the stem becomes gradually thicker.

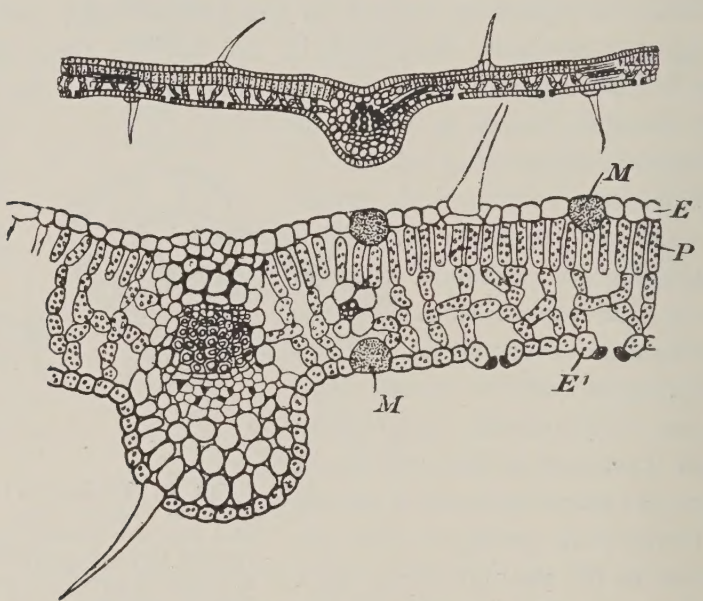


FIG. 58. Transverse section through a portion of the leaf of Elm (*Ulmus campestris*). including a vein. The upper figure is magnified 80 times, and the lower one 300 times. E = epidermis; E' = one of the enlarged epidermal cells which bear the guard-cells; M = mucilage cells; P = palisade layer. Beneath the palisade layer is the spongy parenchyma. In the vein (vascular bundle) the xylem is towards the upper surface, and the phloem towards the lower. The epidermal hairs are unicellular.

The elm stem thus differs from that of the sunflower, in the amount of **secondary tissue** which is deposited by the cambium—that is, in the amount of **secondary growth** or **thickening**. In the sunflower it is comparatively little and is limited; in the elm it is continuous through a great period of time—a hundred years or more, and in the Californian pine may continue through five centuries or even more.

(B.) THE LEAF.

In the main features of its microscopical structure the leaf is similar to those already described, but differs from them in certain minor

details. As in the holly leaf, stomata occur on the under surface only, but they are raised above the general surface of the leaf, by the enlargement of the epidermal cells bearing them (Fig 58, E′). They thus lie upon the epidermal cells, so that when viewed in surface view (Fig. 59, II) the sinuous outline of the epidermal cells can be seen beneath them. Some of the epidermal cells (Fig. 58, M), on both the upper and under surfaces of the leaf, have their cell-walls converted into mucilage, which swells the cells to a great extent; in hæmatoxylin-stained preparations they become stained very intensely and are very conspicuous in consequence. Unicellular epidermal hairs are present on both surfaces, but multicellular hairs are absent. The upper epidermal cells are devoid of chlorophyll grains, but the lower ones each contain a few. The palisade layer (P) is composed of a single row only of cells, which are very loosely packed together. In other features the leaf resembles those of the sunflower, bean, and holly.

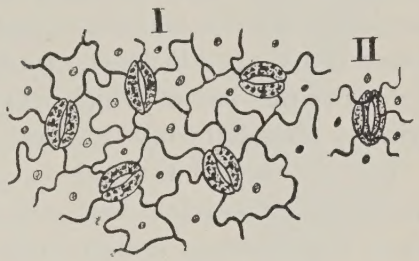


FIG. 59. I. Outer surface view of epidermis of leaf of Elm (*Ulmus campestris*), showing the epidermal cells and the guard-cells of the stomata. II. Inner surface view of a stoma, showing how the guard-cells are supported by the epidermal cells.

(C.) THE ROOT.

The root of the elm is not favourable for the study of minute structure, so we shall substitute that of the horse-chestnut (*Æsculus Hippocastanum*).

Examination of a section of a young fibril, through a portion that is not yet coloured red, will show that it is fundamentally the same as the corresponding portion of the bean root, that lies between the lateral rootlets and the apex. It differs from it principally in the presence of a distinct hypodermal layer situated immediately within the piliferous layer, and characterized by the thickening of its radial walls.

A section through an older portion of the root—for instance, in the region of the lateral rootlets—will show, as in the bean, a withered cortex, which is replaced by a corky layer developed from a cork cambium, that in its turn originates from the pericycle. But the protoxylem groups are united in the centre, so that there is no pith, as in the bean root. In other features, such as the number and

relative arrangement of the primary xylem and primary phloem groups and the origin of the cambium, it is similar to that of the bean. In the mode of origin of its lateral roots it resembles that of *Helianthus*.

Examination of a transverse section through an older portion of the root, will show that secondary xylem and phloem have been formed in precisely the same manner as that in the bean or sunflower root; but the xylem is arranged in concentric rings (annual rings) as in the arboreous stem, the number of which will depend upon the age of the root; the primary medullary rays are small, and there is no pith.

The absence of the pith is, as a rule, but not invariably, the one character by which a very old arboreous root may be distinguished, when examined in section, from an arboreous stem. But not a few arboreous roots possess a small pith, and in many arboreous stems the pith is much reduced, so that it becomes a matter of considerable uncertainty as to whether a given section is of an arboreous stem or root. The real distinction, however, lies in the position of the proto-xylem with regard to the rest of the primary xylem, i. e. at the outer limit in roots and at the inner limit in stems. This is very difficult to determine in old roots or stems. The presence of lenticels would, of course, decide the point, but then lenticels are not always present in the sections through a stem.

The root of the horse-chestnut as an arboreous type, therefore, differs from that of the bean much in the same way that the arboreous stem differs from the herbaceous one, i. e. in the amount of the secondary thickening. The absence of the pith in the one and its presence in the other is not a fundamental difference, for some herbaceous roots possess no pith while it is present in some arboreous ones.

CHAPTER IV

AQUATIC PLANTS

MARE'S-TAIL (*Hippuris vulgaris*).

1. External Characters.

(A.) The Shoot and Root.

In summer and autumn there may be often found in shallow ponds or watery ditches, a green herbaceous plant, characterized by its finely ridged stem and its numerous whorls of leaves at equidistant intervals (Fig. 60). It attains a total length of from 18 inches to

2 feet, the lower part of which is submerged beneath the water, while the upper part, about 8 to 18 inches, projects upwards into the air. Traced downwards, the stem ends in a rootstock which lies buried in the mud and from which numerous roots arise and spread outwards. The stem is annual, but the rootstock is perennial; that is, the stem dies down every year, but the rootstock lives year after year, and sends up fresh stems in each successive season. The stem, like most aquatic ones, is pliant and easily damaged by rough treatment, and it is buoyant and floats with ease in the water. The leaves are linear, thin, and with entire margins, the latter character serving to distinguish this plant from the water milfoil (*Myriophyllum*), which in general habits closely resembles it. The leaves on the submerged part of the stem are much longer—in deep streams often 2 or 3 inches long—than those on the aërial part, which may be less than half an inch in length; the transition from the lower to the upper leaves is gradual. The number of leaves in each whorl varies from 8 to 12.

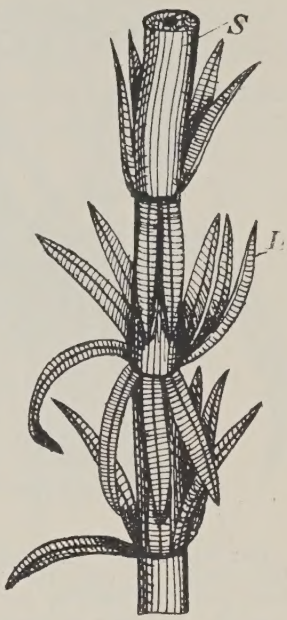


FIG. 60. A portion of the aërial stem of the Mare's-tail (*Hippuris vulgaris*). Natural size. L = leaves; S = stem.

(B.) THE FLOWER AND FRUIT.

We have seen (supra, p. 78) that in the flower of the elm, the perianth is reduced to an almost inconspicuous green and membranous investment, devoid either of bright colours or sweet scents. The flower of the mare's-tail is still more reduced, for the perianth (Fig. 61, C) is represented by a barely perceptible rim near the summit of the ovary. The flowers are small, inconspicuous, and lodged in the axils of the upper whorls of leaves (Fig. 61). Each flower consists of a single carpel (O) and stamen (S). The ovary is globular or oblong in form, and from its summit a thread-like style (ST) covered with small hairs projects. There is no definite stigma, for the whole surface of the style serves for the adhesion of the pollen, and we may say therefore that the stigmatic surface is diffuse. The ovary contains a single compartment, in which a single ovule is suspended.

The androecium is represented by a single stamen (S), which arises from the rim surmounting the ovary. It consists of an anther and a very short filament.

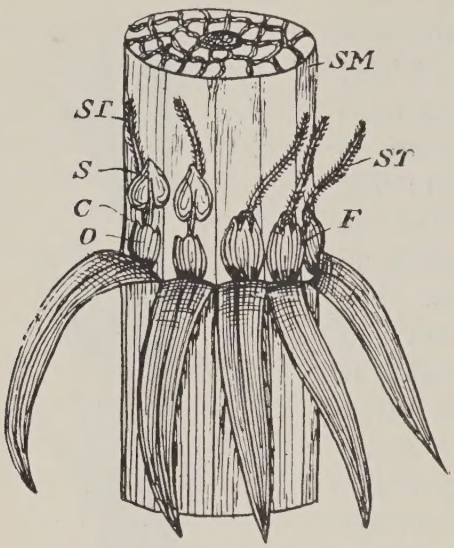


FIG. 61. A portion of the stem of the Mare's tail, bearing the floral organs. Enlarged two and a half times. C = perianth; F = fruit; O = ovary; S = stamen; SM = stem; ST = stigma.

The fruit (F) which results from the maturation of the ovary and ovule, as the result of fertilization, is an oblong, small, one-seeded body, with a hard outer wall. When quite ripe, in late autumn, it falls into the water, and is carried by currents for a greater or less distance from the parent plant, and ultimately sinks into the muddy floor. Here it remains dormant until next spring, when it germinates and grows into a new plant.

2. Internal Structure.

(A.) THE STEM.

The distinctive feature of aquatic stems is the large size of the intercellular spaces and the reduction or absence of the xylem. In the mare's-tail the xylem is reduced in quantity, but in the water-lily it is absent.

Examination of a transverse section (Fig. 62) of the stem shows a well-defined **epidermis**, from some of the cells of which, flat, scale-like hairs arise; the outer surface of the outer wall of the cells is altered to form a thin cuticle. Within the epidermis is a broad band of parenchyma, composed of somewhat elongated chlorophyll-containing cells, so arranged as to leave very large intercellular spaces, much bigger than the cells themselves; this is the **cortical parenchyma**, and since its intercellular spaces are filled with gases, it serves to render the stem buoyant. At the nodes, the stem is strengthened by the presence of **diaphragms** or horizontal plates composed of a single layer of cells, arranged across the intercellular spaces. The innermost layer of the cortex is composed of small

cells forming a well-marked **bundle sheath** or **endodermis**, within which is a not very definite layer forming the **pericycle**, which surrounds the central vascular cylinder or stele. This latter consists of strands of elongated, thin-walled vessels of the nature of bast (phloem) lying immediately within the endodermis ; within this is an interrupted ring of xylem strands, composed of small vessels with lignified walls ;

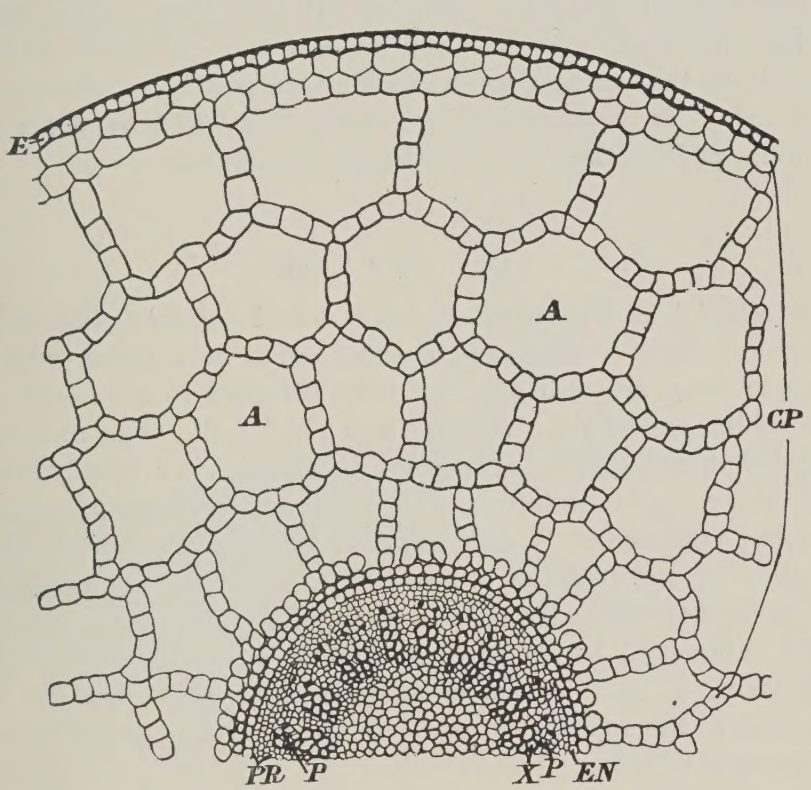


FIG. 62. Portion of a transverse section of stem of the Mare's-tail (*Hippuris vulgaris*). Magnified 300 times. A=air-space ; CP=cortical parenchyma ; E=epidermis ; EN=endodermis ; P=phloem ; PR=pericycle ; X=xylem.

centrally and passing in between the xylem strands is ordinary thin-walled parenchyma, forming a medulla or pith.

The stem of *Hippuris* differs therefore from the terrestrial ones, in that it has a relatively very large cortex, while the single stele is axial in position. The cortex is spongy in nature, the intercellular spaces being large and filled with gases, so that we can now understand the soft nature of the stem and the buoyancy which it exhibits when submerged in water. The reduction in the quantity of the xylem is not difficult to understand if we remember that this tissue is the

channel along which, in terrestrial plants, the water and dissolved mineral salts taken up by the roots pass upwards to the leaves. In a plant which is in contact at nearly every part of its surface with the water and its contained salts, absorption can go on all over the submerged surface, and the necessity for special channels disappears. But *Hippuris* is not wholly submerged, for some parts of it project upwards beyond the water into the air, and these parts must be supplied with water and dissolved mineral salts by means of special channels, so that we find some considerable portion of xylem present in the stele. In plants which are wholly submerged, as in the water-lily (infra, p. 102), the xylem completely disappears.

(B.) The Leaf.

The aërial leaves of *Hippuris* show a well-defined **epidermis** with a well-developed cuticle, and stomata upon both upper and lower surfaces; there are also disc-like hairs attached to the epidermis by short stalks, the whole consisting of a single cell. The mesophyll is composed of a **palisade layer**, the cells of which are loosely arranged beneath the upper epidermis, and a **spongy parenchyma** towards the lower epidermis. Several vascular bundles are present lying in the plane at the junction of the palisade and spongy parenchyma, and the median one is larger than the others.

The submerged leaves in their minute structure differ from the aërial ones, in the absence of stomata from either surface, in the reduction of the mesophyll to a few layers of spongy tissue, and in the presence of a single bundle only.

The aërial leaves of *Hippuris* thus resemble, in the main features of their minute structure, those of terrestrial plants, while the submerged ones are adapted to an aquatic life. The stomata (supra, p. 62) are organs for respiration and transpiration, that is, for taking in air and giving off CO_2 and waste water, and obviously such organs would be of no use on submerged leaves. The disappearance of the palisade layer and the retention of a spongy parenchyma, is adapted to rendering the leaf as buoyant as possible.

THE WHITE WATER-LILY (*Nymphæa alba*).

1. External Characters.

(A.) The Shoot and Root.

Water-lilies are widely spread all over the world, and are to be found floating on shallow, still, or gently running waters in almost all parts.

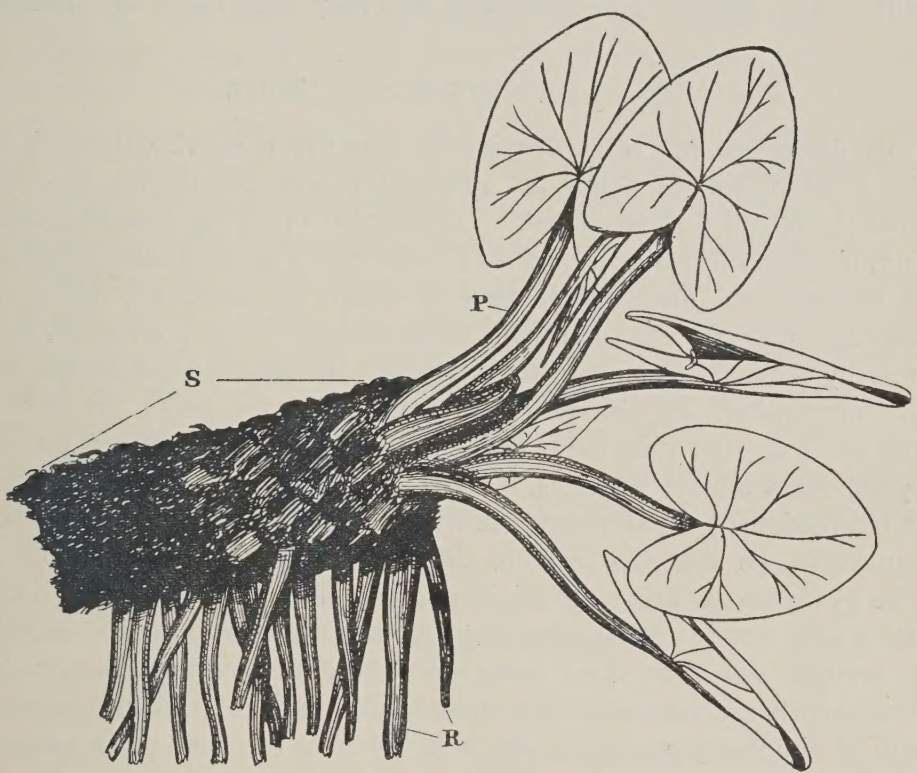


FIG. 63. The rhizome and young leaves of the current year of the White Water-lily (*Nymphæa alba*). One-third natural size. P = petioles of the young leaves; they grow to be much longer; R = roots; S = rhizome or underground stem.

In Britain there are only two genera, the white water-lilies (*Nymphæa*) and the yellow water-lilies (*Nuphar*), and in each genus there is but a single species. Both genera are aquatic herbs, with a thick, fleshy, prostrate stem (rootstock or rhizome) (Fig. 63, S), that is buried in the mud, and from which numerous rather thick roots (R) arise. From this submerged stem the very long, ascending leaf-stalks (P) (petioles) also take their origin, and ascending, bear at their outer extremities large heart-shaped, glabrous leaves, about 6-8 inches in

diameter, which float on the surface of the water. The leaves of the current year are borne around the apex of the stem, and the decayed bases of the previous year's leaves can be seen along the remainder of its length. The flowers are large, usually 3-4 inches in diameter, and solitary (one only to each flower-stalk). In *Nymphæa* they are white, scentless, and float on the surface of the water, but in *Nuphar* they are yellow, slightly scented, and are raised two or three inches above the level of the water. The size of the flower varies considerably in both genera, and in other characters also they seem liable to variation.

(B.) The Flower and Fruit.

In *Nymphæa* the calyx consists of four green sepals arising from the floral receptacle below the gynæcium, each sepal being separate from the others (polysepalous). The number of sepals, though usually four, is subject to variation and may be more. The petals are indefinite in number and arranged in several whorls or envelopes, the outer ones being as large as the sepals, while the inner ones are smaller and pass by gradual stages into the stamens. In *Nuphar* the sepals are five in number, greenish-yellow in colour, and the petals are yellow and much smaller than them. The androecium consists of indefinite[1], hypogynous, adnate stamens, inserted with the petals on the outside of the thickened floral receptacle which is raised upwards round the gynæcium, so that the stamens and petals are almost perigynous. The gynæcium at first sight might possibly be regarded as syncarpous, but it is in reality apocarpous, since the apparent fusion of the carpels is brought about by their being embedded in the floral receptacle. The carpels are not themselves united, but are each sunk in a depression of the fleshy receptacle which is adherent to them. The carpels are numerous in number and elongated in the radial direction, and each one is crowded with very numerous ovules attached over the whole of the inner surface of its wall, so that the placentation is described as **superficial.** The whole of the floral head with its embedded carpels forms a sub-conical mass, and the stigmatic rays are arranged in a radiating manner, round the blunt apex of the cone; each ray is prolonged into an erect, linear, and incurved appendage, and in position lies immediately above the middle of the cavity of each carpel. Such flattened stigmas are technically described as **capitate**, and such a kind is to be found in the common

[1] See chapter XXV, p. 476, for definition of terms.

garden poppy. In the poppy, however, the gynæcium is syncarpous, while in the water-lily it is apocarpous, and we find that there is a correlated difference in the relation of the stigmatic rays; in the latter plant, as we have already seen, the rays correspond in position to the middle of the cavity of each carpel, but in the former plant they lie above each of the numerous septa which partially divide the cavity of the ovary into compartments, and like them are double in nature.

The fruit is pulpy and indehiscent, and botanically considered is a **spurious** [1] one, since it is composed of other parts of the flower besides the ripened carpels; the floral receptacle in which these are embedded becomes enlarged and succulent as the fruit ripens, so that the fruit consists of the pulpy floral head and ripened carpels. The apple and strawberry are other spurious fruits of this kind, in which the thalamus (floral receptacle) takes part in their formation.

The seeds which are contained within the fruit and result from the ripening of the ovules, are exceptional in that they contain both perisperm and endosperm, which are nutritive tissues, the contents of which are absorbed by the embryo during the very early stages of its development. Some seeds contain neither of these tissues, while others contain one or the other, but it is only a very few that contain them both. The precise nature of perisperm and endosperm is explained on pp. 133 and 138.

2. Internal Structure.

(A.) The Stem (Rhizome).

The rhizome is a thick fleshy organ, and if we cut one through along its length in the middle line, and examine the cut surface (Fig. 64, I), we shall see that it is limited externally by a brownish coloured band of tissue (E), which when microscopically examined is seen to be composed of an outer layer of oblong cells, constituting the **epidermis**, and of several (6–8) layers of very small-celled parenchyma. Many of the epidermal cells are prolonged into unicellular hairs, and in fact so numerous are these that the surface of the stem is soft and velvety to the touch in consequence. The epidermal cells contain nothing but the living protoplasm, while the immediately subjacent layers of cells possess starch grains in addition. The zone

[1] See chapter XIX, p. 317, for definition and variety of fruits.

of small-celled parenchyma passes somewhat abruptly into a broad trabecular cortex (C) composed of parenchyma with very large intercellular spaces, identical with that in the petiole (Figs. 65 and 66, TP). When a tissue is composed of cells arranged in trabeculæ so that these bound large spaces, it is called **trabecular tissue.** This kind of tissue is very characteristic of all aquatic plants throughout the vegetable kingdom. The cells of this tissue in the stem of *Nymphæa* are crowded with starch grains, and to a large extent the

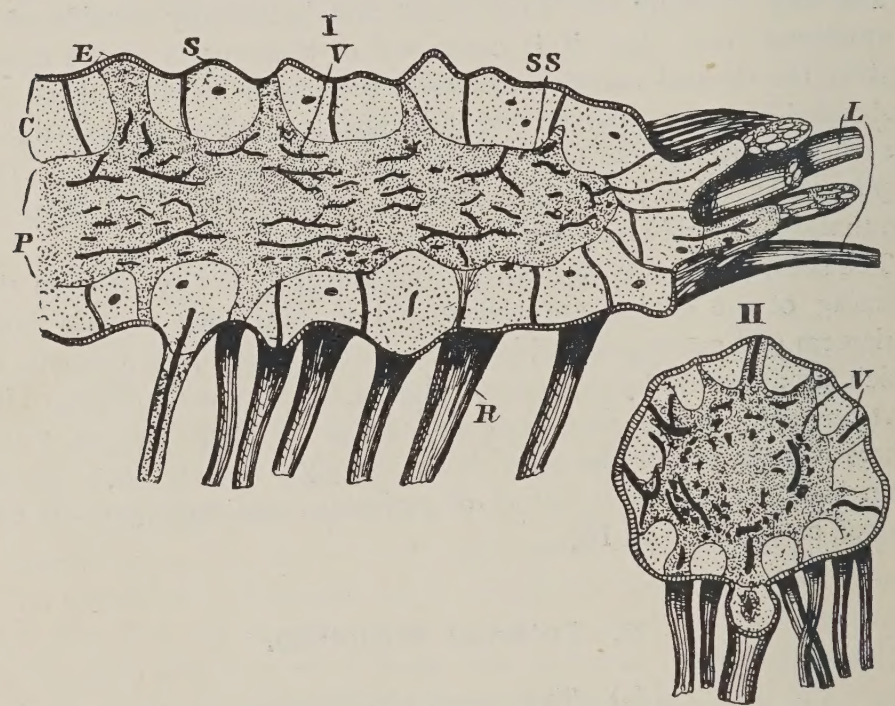


FIG. 64. Preparations of the rhizome of the White Water-lily (*Nymphæa alba*) to show its internal structure. I. A median longitudinal section. II. A transverse section. One-third natural size, and examined by the unaided eye. C=cortex; E=epidermis and a band of small-celled parenchyma belonging to the cortex; L=bases of the petioles; P=pith (intra-stelar tissue); R=bases of the roots; S=strengthening strands of very small-celled parenchyma; SS=stelar sheath (pericycle and endodermis); V=vascular bundles.

parenchyma in aquatic plants replaces the sieve-tubes of terrestrial forms, and serves as the channel along which food-material may travel from part to part. Occupying the core of the stem is a mass of parenchyma (P), the cells of which have relatively thick cellulose walls, and very small intercellular spaces ; the cells of this tissue are also densely crowded with starch grains, and like those of the cortex serve for the storing and transmission of food-substances. The trabecular cortex (C) is strengthened at frequent intervals by plates (S) of

very small-celled and compact parenchyma, which serves also to retain the central core in position.

The vascular bundles (Fig. 64, V) are embedded in the central mass of parenchymatous ground-tissue, and are arranged in two concentric layers (II) ; they very freely anastomose with one another, so that as seen in a longitudinal section of the stem they form a network with somewhat open meshes. From this double cylinder of bundles, branches pass out to the roots (R) and to the leaves (L). The structure of the vascular bundles exhibits a very reduced condition, for neither phloem nor cambium is present, and the xylem consists of a few narrow vessels, but slightly lignified and their walls marked with broadly reticulate thickenings ; the rest of the bundle consists of small-celled parenchyma, equivalent to the conjunctiva of terrestrial forms.

The endodermis and pericycle, collectively forming the stelar sheath (SS), are not very clearly distinguished by microscopical examination ; but the limits of the stele are very obvious to the naked eye on the cut surface of a bisected stem (Fig. 64, SS), owing to the sudden transition from the compact intra-stelar tissue (P) to the porous tissue of the cortex (C). The stem is thus **monostelic**, since the whole of the vascular bundles are enclosed within a common stelar sheath.

(B.) The Petiole.

In its minute structure the petiole, like the rhizome, is characterized by the presence of trabecular tissue and a reduced condition of the vascular bundles. Externally it is limited by a single layer of squarish cells forming the epidermis (Figs. 65 and 66, E), and which are devoid of chlorophyll grains. Stomata are absent, since they are obviously of no use on organs submerged in water. Within the epidermis is a band of parenchyma some five to seven layers thick, composed of squarish cells immediately subjacent to the epidermis, but of elongated ones in the more centrally situated layers. This band of tissue constitutes the cortex, and its cells are laden with chlorophyll grains. Within the cortex the petiole is composed of trabecular tissue (T.P), with very large air-spaces, in the angles of many of which are peculiar hairs (IH) ; these from their position are called **internal hairs**, and each consists of a base or foot which pierces one of the stellate cells, and from which three short prongs project, each being trifurcate at its free extremity. The function of these hairs is unknown.

The vascular bundles (Fig. 65, VB) are arranged in two consecutive rings, an outer and inner, and each one is surrounded by its own endodermis (Fig. 66, EN) and pericycle (P), so that the petiole (leaf-stalk), unlike the stem, is **polystelic.** Each bundle contains a little phloem (PH) and some of them a few xylem vessels (XV) which are but very little lignified and marked with reticulate markings. The xylem is thus exceedingly reduced and in some bundles is absent altogether. Functionally its place is taken by two (in some bundles one only) tubular cavities (T.C) lined with a regular epithelium of paren-

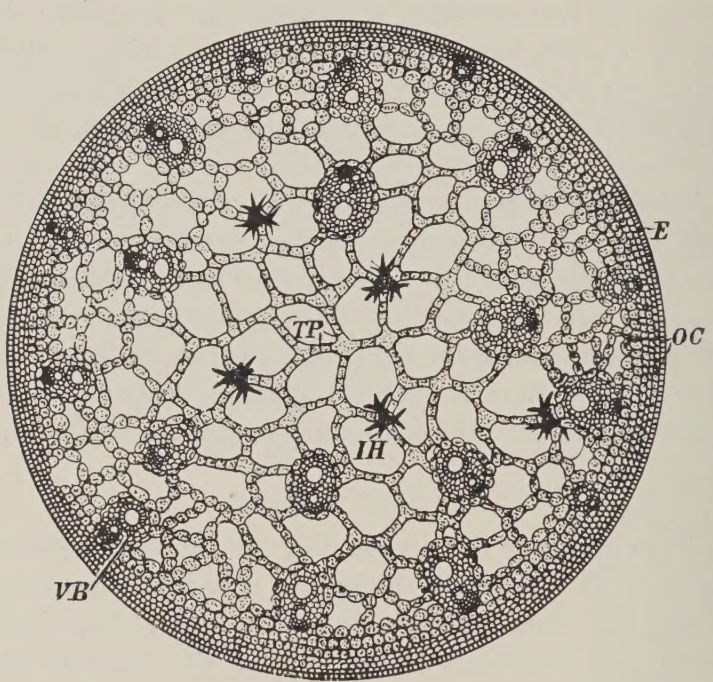


FIG. 65. Transverse section of the petiole of the White Water-lily (*Nymphæa alba*). Magnified 80 times. E = epidermis; IH = internal hair; OC = cortex; TP = trabecular tissue; VB = vascular bundle.

chyma with unlignified walls. The rest of the bundle is composed of conjunctive parenchyma.

The arrangement of the bundles in both the stem and the petiole thus differs from the typical dicotyledonous condition in that they are not confined to a single circle, but have additionally another series of bundles within the outer one, and which thus come to lie in the central portion of the ground-tissue; bundles thus situated in the medulla or pith of a stem are called **medullary bundles,** and are a constant feature in the arrangement of the vascular strands in monocotyledonous stems, but are exceptional in those of dicotyledons.

They further differ from the typical dicotyledonous condition in the absence of cambium, which is a constant feature in the bundles of monocotyledons; such bundles are said to be closed.

Compared with *Hippuris*, *Nymphæa* is a more thoroughly aquatic type, and the much greater reduction of the xylem and phloem in its vascular strands is correlated with this difference in habit.

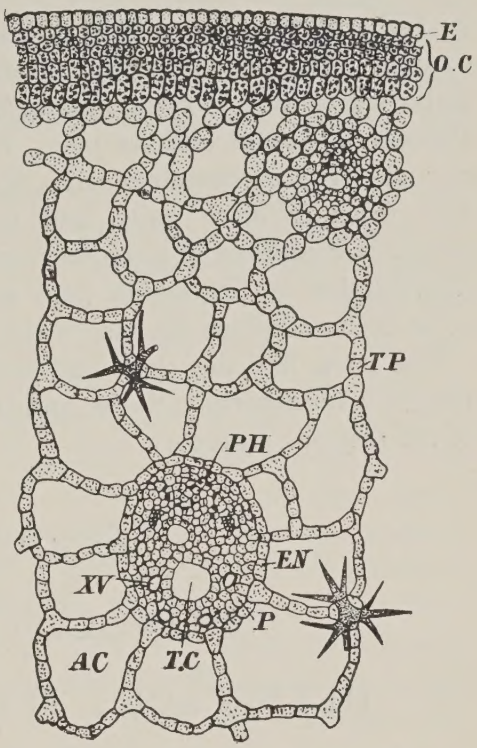


FIG. 66. A portion of the petiole of the White Water-lily, more highly magnified (300 times). AC = air cavity (intercellular space); E = epidermis; EN = endodermis; O.C = cortex; P = pericycle; PH = phloem; T.C = tubular cavity; T.P = trabecular tissue; XV = xylem vessels.

(C.) THE LEAF.

The chief distinctive features of the leaf are the absence of a palisade layer and of stomata. Examination of a transverse section shows it to be limited by an upper and a lower epidermis, the cells of the former containing chlorophyll grains, while those of the latter are for the most part filled with a red fluid and are devoid of chlorophyll; here and there, however, in the lower epidermis, cells, either singly or in small groups, are to be seen which contain chlorophyll but not any red sap. The reddish-brown colour of the under surface of the leaf is due to the coloured cell-sap. Stomata are absent from both surfaces. Between the two epidermal layers is the spongy mesophyll, the upper layer of which (that immediately beneath the upper epidermis) is composed of regularly arranged and closely packed cubical cells and which may therefore represent a palisade layer; its cells are very densely crowded with chlorophyll grains, more densely than the remaining spongy portion of the mesophyll. Near to the midrib very large air-spaces are developed, and the tissue becomes decidedly trabecular and bears internal hairs. The vascular bundles are similar to those of the petiole.

(D.) The Root.

In the general arrangement of its parts the root of *Nymphæa* is like that of a terrestrial herb (*Phaseolus*), but it is characterized by its trabecular cortex and by the possession of eight primary xylem strands. The primary xylem is arranged in radial strands within the stelar sheath and is composed of vessels similar to those of the stem. Phloem is absent and its place is occupied by small-celled parenchyma. The epidermis consists of a single layer of well-defined cells with thick cellulose walls, and immediately subjacent to this the cortex is composed of some four or five layers of parenchyma without intercellular spaces, which pass somewhat abruptly into the trabecular tissue of which the rest of the cortex consists.

The root, like the stem and petiole, is thus characterized by the presence of trabecular tissue, and to a lesser extent by the reduction of the vascular strands.

CHAPTER V

MONOCOTYLEDONS

HERBACEOUS TERRESTRIAL TYPE

THE MAIZE-PLANT (*Zea Mais*).

1. External Characters.

(A.) The Shoot and Root.

The maize or Indian corn-plant is a native of America, but has been introduced into some of the Indian islands where it is largely cultivated; in Britain it is cultivated chiefly for garden purposes, its erect stem and gracefully curved leaves serving to relieve the monotony of a more familiar vegetation. It belongs to the great family or order of plants characterized by the peculiar structure of their flowers, called grasses, and to which belong also the oat, wheat, rye, barley, rice, mat-grass, feather-grass, &c. It is chosen here as the type of a monocotyledonous herbaceous plant, partly because of the facility with which it can be grown from seeds and therefore easily obtainable at all stages of its growth, partly because it serves, on account of the comparatively large size of its flowers, as an introduction to the study

of the morphology of those of the other grasses—ever a difficult study to the beginner—and partly because the minute structure of the stem is typical and all the essential features are very clearly represented. The flower of *Zea Mais* is not typical for the class of monocotyledons, but these differ from those of dicotyledons mainly in the number of their parts and in the development of the embryo, and such other differences as they exhibit are considered on pp. 139, 295, 344, and 356.

A fully developed plant of *Zea Mais* may attain a height of six feet or more. The stem itself is hidden by the ensheathing bases of the leaves, but when these are removed it reveals a uniform thickness along its length, except above the fifth or sixth node, where the thickness becomes diminished with every succeeding node, but remains uniform for each internode. This uniformity of thickness is correlated with the absence of an internal cambium, so that once the stem has reached its full growth it cannot become thicker by the deposition of new tissue, such as occurs in dicotyledonous stems. With but few exceptions monocotyledonous stems can only increase in length—not breadth, except to a limited extent as mentioned below—and as this takes place through the activity of the apical meristem, it follows that if the activity of this is uniform the breadth of the stem will be also uniform. The fact that the upper internodes are not as thick as the lower ones is due to the fact that, after the tissues are laid down, they increase slightly in bulk by the growth of their individual cells and not by the addition of new ones, hence the lower nodes are thicker than the upper ones. But this growth is limited, and by the time that the lower internodes have reached their full development the upper internodes are still growing, and eventually become as thick as the lower ones ; and, having reached their full development they also will cease to grow. Thus the uniformity of the thickness of the stem is maintained. The degree of thickness will depend upon the degree of activity of the apical meristem.

Upon the surface of a stem carefully stripped of its leaves the internodes will be seen to be very long—a somewhat uncommon feature among monocotyledons—and the nodes to be equidistant, with the exception of the first few upper ones, where they closely succeed one another. As we shall see in the sequel, this difference in the length of the internodes (which is of course only temporary, disappearing as growth proceeds) results in a slight difference in detail in the arrangement of the vascular bundles.

The leaves are elongated and lance-shaped (**lanceolate**) in form, with entire margins fringed with short, stiff hairs. They are sessile, i.e. attached directly to the stem, and sheathing along their lower fifth; in the lower portion the sheath completely invests the stem, and the node is marked by a circular ridge where the leaf is inserted; at the upper part of the sheath, at the point where the leaf diverges from the stem, there is a membranous band-like outgrowth arising from its upper surface called the **ligule.** The lamina is traversed throughout its length, along the middle line, by a very pronounced midrib, which seen from the upper surface is indicated by a broad white line. The venation is parallel, i.e. the principal veins run parallel to one another and do not branch to form a network in the intervening spaces; the principal veins are, however, connected with one another by means of small cross connexions here and there. The absence of a reticulate venation (network of veins) such as is present in the leaves of dicotyledons, is very characteristic of monocotyledons, though it is not diagnostic; for there are a few monocotyledons, such as herb Paris (*Paris quadrifolia*), which possess a reticulate and not a parallel venation. The leaves are alternate, with a phyllotaxis of one-half. In the axil of each leaf a flowering branch arises, and if the plant is a young one the leaves must be stripped off to see the undeveloped bud in their axils.

The root is a **fibrous** one, i. e. arises from the base of the stem in many nearly equally developed axes. There is not a main (tap) root continuing the axis of the stem, as in dicotyledons. From the internode just above the first node, above the base of the stem, and in older plants also from the internode immediately above the second one, a ring of lateral roots arise which pass at once downwards to the soil; these serve to give the plant greater support, and contain much more sclerenchyma, or strengthening tissue, than the underground roots.

(B.) The Flower and Fruit.

The flowers of the maize are borne upon the terminal portion of the main stem and upon lateral branches arising from the axils of the leaves. Each of these flowering axes (Fig. 67, I) itself bears secondary branches. The flowers are borne upon them in a dense cluster, the youngest flower being at the apex and the oldest at the base.

The flowers of the maize are specially modified and cannot be

regarded as typical ones; they are, however, very characteristic of the family of grasses (*Graminaceæ*). They are unisexual, and the two sexes are borne upon different flowering branches; the male flowers are stalked (I) and the female (II) ones sessile. If we examine a ripe male inflorescence (Fig. 67, I) we shall find that it is composed of a number of stalked bodies, each containing (Fig. 68) two prominent green scales (OG) with three elongated (MS) straw-coloured structures projecting from between them and borne upon long slender filaments. Such a body in reality contains two male flowers, of which one (MS)

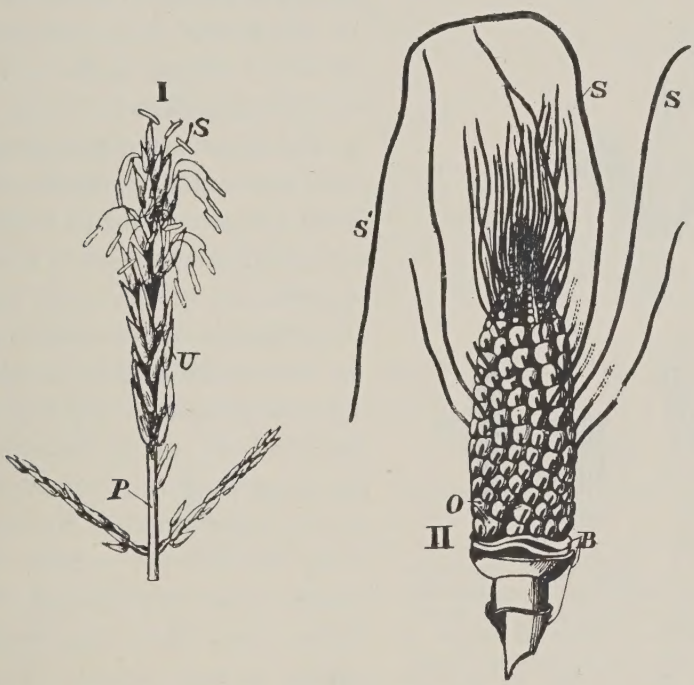


FIG. 67. I. A male flowering branch of the Indian Corn-plant (*Zea Mais*). P = peduncle; S = protruded stamens of ripe flowers; U = unripe flowers. II. A female flowering branch of the same plant. B = bracts; O ovaries; S = style; S' = stigma.

ripens before the other (US). The two prominent green, membranous, lance-shaped scales (OG) are called the **outer glumes**, and if we move these aside we shall find two other pairs of white, lance-shaped scales within. These are the **flowering glumes** (FG) and **paleæ** (P), and in the unripe flower, each pair, consisting of an upper, larger glume, and a lower, smaller pale, encloses three stamens (US) with very short filaments; but as the stamens ripen, the filaments elongate very considerably, and carry the anthers far out from between the flowering glume and pale, the anthers hanging pendent upon the

filaments. The anthers are the three elongated, straw-coloured bodies mentioned above; and those of the second flower are as yet unripe and still enclosed within the flowering glume and pale, and by the time that they have ripened the others will have withered. On either side of the filaments at the point where they arise from the pedicel (the little flower stalk) (S), and between the glume and pale, and alternating with them, is a little semi-crescentic scale called a lodicule (L); they probably represent a much reduced perianth.

The female inflorescence (Figs. 67, II, and 69) is a much bigger one than the male. To see all the parts of the flower it is necessary to examine a young inflorescence—one still enveloped in its bracts (B), which in the figure are represented only by the bases, the other parts having been cut away—for at a later period cohesion of some parts and the disappearance of the style take place. The female inflorescence is borne on one of the axillary branches, and up to a comparatively late period is invested in many leaf-like bracts (B); its position, however, can be easily determined by the tuft of very long filamentous organs (S) which project from the apex of the bud of bracts, and which are the elongated styles of the carpels. The flowers are borne sessile upon a thickened axis, and are very closely packed together. Each flower is invested in two outer glumes (Fig. 69, OG), a flowering glume (FG) and pale (P); and there are no lodicules as in the male flower. But there are two sterile glumes (SG) lying between the upper outer glume and the flowering glume, and so called because they contain no ovary between them; they probably represent a second flowering glume and pale. Between the flowering glume (FG) and pale (P) is the somewhat spherical ovary (O) with a single, very elongated style (S) passing forward from its summit. The style is remarkable for its length, attaining to from four to six inches, at the time when the ovary itself is not more than a tenth of an

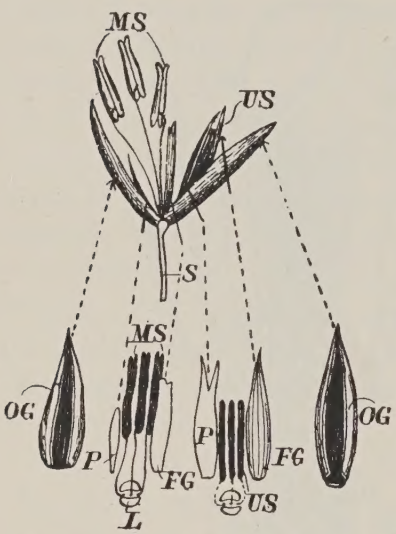


FIG. 68. The upper figure represents a male flower with the parts opened out. The lower figure represents the flower dissected and its parts arranged in successive order. FG = flowering glume; L = lodicules; MS = mature stamens; OG = outer glume; P = paleæ; S = pedicel; US = immature stamens.

inch long; it is further exceptional in that it is single, all grasses with but a few exceptions having two styles to each female flower. The wall of the ovary is thin, and encloses a single ovule only, which is sufficiently big to quite fill the cavity of the ovary, with the walls of which it is in contact. As the fruit ripens, the wall of the ovary fuses with the outer integument of the ovule, so that a grain of Indian corn is not a seed, as popularly and erroneously called, but a modified fruit, called by botanists a **caryopsis**. The fruits of all grasses are of this nature (infra, p. 318, and Fig. 170, IX). Strictly considered, a seed is a ripened ovule, but the so-called 'seed' of Indian corn is the ovule plus the ovary, and botanically, therefore, is a fruit.

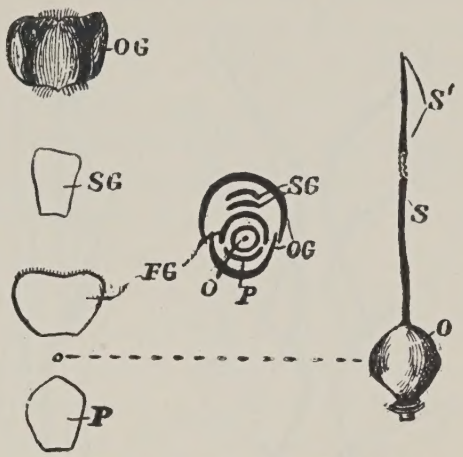


FIG. 69. A female flower with its parts dissected out and arranged in order. The central figure is diagrammatic and represents a cross section through the flower, and shows the arrangement of the parts. FG = flowering glume; O = ovary; OG = outer glume; P = pale; S = style; S' = stigma; SG = sterile glumes.

2. Internal Structure.

(A.) The Minute Structure of the Stem.

The course of the vascular bundles in the stem of the maize is very different to that in the stems which we have already studied, and the difference is one which distinguishes the whole class of the monocotyledons from the dicotyledons.

If we examine some thick median sections of the apex of the stem (Fig. 70, I), we shall find that the numerous veins coming in from the leaves proceed toward the centre of the stem, becoming thicker as they do so, but before quite reaching it they turn downwards and gradually approach the periphery again, becoming thinner as they proceed. It follows from such an arrangement that in a transverse section through this region of the stem we shall see the thicker portions of the bundles disposed centrally with the thinner parts of the bundles coming down from higher parts of the stem, arranged peripherally to them. This arrangement of the bundles is one found in monocotyledons, such as palms, which have very short internodes,

and in the apices only of those stems with long internodes. In palms, too, it is only the larger bundles from the leaf which pass towards the centre of the stem, the smaller ones turn downwards in the stem at once, so that the bundles near the periphery are more crowded than in the centre. But in the stem of *Zea Mais*, which has very long internodes, the characteristic arrangement found at the apex becomes modified in the older portions of the stem (Fig. 70, II), for here the bundles run an almost straight course, and at the nodes (N) a complex anastomosis of the bundles coming from the leaf is formed with those of the stem, and of these latter with each other. A transverse section through any portion of one of the internodes (Fig. 71) will show the thicker portions of the bundles (LB), aggregated not in the centre as in the palm type, but in a more or less regular ring or zone within the cortical region, with the thinned-out portions (SB) of the bundles that entered the stem at a much higher node, in part without but mostly within this zone.

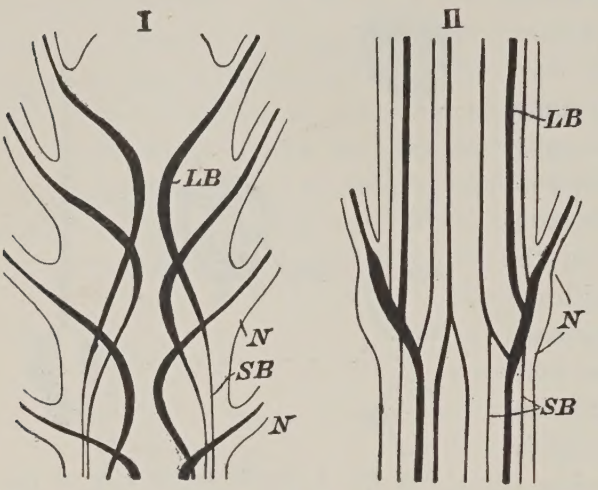


FIG. 70. Showing the course of the vascular bundles in a Monocotyledon. I. The course of the bundles as they run in the apex of the stem of *Zea Mais* and throughout the whole length of the stem in Palms. II. The course of the bundles through the length of the stem of *Zea Mais*. LB = the thickened part of the vascular bundle coming in from the leaf at the node immediately above; N = node; SB = thinned portion of the bundle coming in at the second or higher nodes above.

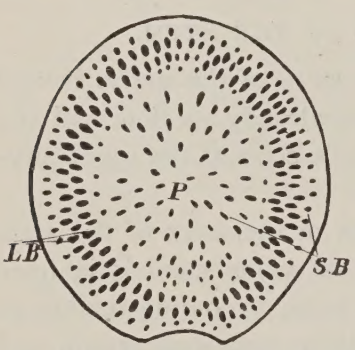


FIG. 71. A transverse section through the stem of *Zea Mais*. Twice natural size. LB = thicker parts of the vascular bundles (see Fig. 70); P = pith or medulla; SB = thinner portions of vascular bundles.

Detailed examination of a transverse section (Fig. 72) of the stem taken from the upper part of one of the lower internodes, will show that it is limited by a definite, though small-celled, epidermis (E), with a well-developed cuticle, and containing stomata (S) here and there. Within the epi-

dermis is a ring (SL), many layers thick, of sclerenchyma, the elongated cells of which have very thick walls; but beneath the stomata the continuity of the sclerenchyma is interrupted by small respiratory cavities (intercellular spaces), in order that a free interchange between the gases within the plant and those of the air may take place. Centrally, the section is composed of thin-walled parenchyma (Figs. 71 and 72, P) with intercellular spaces, the cells in the outer layers of which are rich in protoplasm and chlorophyll granules, while those of the central portion contain less.

Scattered through the substance of the central parenchyma are the vascular bundles (Fig. 71, LB and SB), arranged in a manner already described. The position of the constituents of each bundle, relatively to the centre of the stem, is fairly constant. Each vascular bundle, one of which is represented in detail in Fig. 72, is surrounded by several layers of sclerenchyma (SL'), which serve not only to strengthen the stem, but to protect the bundles should the stem be injured. Within this is the xylem (X), phloem (PH), and xylem parenchyma, but no cambium. The absence of the cambium is characteristic of the vascular bundles of monocotyledons, and it results from this, that once formed the bundles cannot increase in size; hence they are called **closed bundles**. We have already learned that in the dicotyledon increase of the thickness of the stem is mainly the outcome of the formation of new wood and bast by the activity of the cambium. And since in nearly all monocotyledons cambium is absent, and secondary xylem and phloem are not formed, the stem itself cannot increase in thickness, and hence the uniform diameter of a stem of monocotyledons throughout its length.

The xylem is composed of four large vessels, tracheides and xylem parenchyma, which are arranged in the form of a V, with the apex towards the centre of the stem. Two of the vessels are smaller, and these are situated one behind the other at the apex; of these, the more central one is an annular vessel (Fig. 72, AV) and the other a spiral one (SV). The other two vessels (P.V) are much larger, have thinner walls with bordered pits, and are arranged one at either extremity of each arm of the V. In the re-entrant angle of the V and surrounding the vessels are a number of tracheides, with thickened, pitted, and lignified walls, small cavities, and no cell-contents. The annular vessel is usually surrounded by a large air-space, formed by splitting of the xylem parenchyma, which is situated between the vessel and the investing sclerenchyma ring; spaces thus formed are

called **schizogenous air-spaces.** These spaces, however, are found in the more central bundles, and so are not represented in the one figured, which is one of the outer bundles.

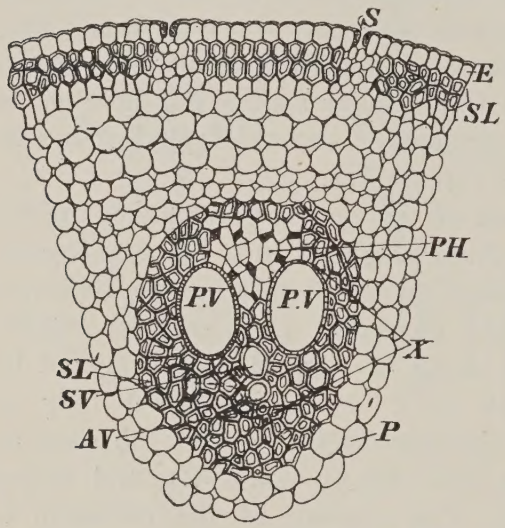


FIG. 72. A small portion of a transverse section of the stem of *Zea Mais*, including a vascular bundle. AV=annular vessel; E=epidermis; P=parenchyma; PH=phloem; P.V=pitted vessels; S=stoma; SL=sclerenchyma; SL′=sclerenchyma investing vascular bundle; SV=spiral vessels; X=xylem.

The phloem (PH) lies in the open angle of the V between the pitted vessels, and is composed of large sieve-tubes and smaller companion cells, filled with protoplasm. It is in all essential characters similar to that of the dicotyledon, except that it has no phloem parenchyma.

The vascular bundles of the monocotyledon as represented in *Zea Mais*, contain the same constituents arranged in the same way as those of the dicotyledon, and the only constant difference between them is that the vascular bundle of the dicotyledon is an open one, i.e. contains a cambium, while that of the monocotyledon does not, and is therefore a closed one. In some monocotyledons, as in the banana, the bundle is not collateral as in *Zea Mais*, but concentric, i.e. the xylem surrounds the phloem. This is also the case in some of the bundles of some dicotyledonous stems.

(B.) THE LEAF.

As already observed, the leaf of the maize is a very long one, sufficiently so, that it would bend under its own weight, were it not in some way supported. Hence we shall expect to find in the internal structure of this leaf some arrangement of tissues, which we have not hitherto met with in the leaves which we have so far studied.

Examination of a transverse section of the leaf (Fig. 73, I) shows its outline to be sinuous, due to the presence of strands of strengthening tissue (S), lying along the upper and under surfaces of the vascular bundles (V). Covering both surfaces of the leaf is a well-defined

epidermis (II, E), bearing conical hairs (H) and stomata (ST), with guard (G) and subsidiary (SB) cells. If a piece of the epidermis of the leaf be stripped off (Fig. 74) and examined in water, from a surface view, it will be seen that the epidermal cells (E) are oblong in form, with wavy outline; and between the ends of some of these are two elongated, curved guard-cells (G), surrounding the pore of the stoma, and on the outer side of each of these (upon their convex surface) is a triangular subsidiary cell (SB). If a piece of the epidermis be treated with nitric acid, dried and ignited on platinum foil, and the ash examined under the lower power of the microscope, it will be found that the cells retain their form. If the ash be treated with acetic, nitric, or hydrochloric acids, there is no evolution of gas and the ash does not dissolve; it is, therefore, probably composed of silica, which thus forms a skeleton of the epidermal tissue. Chemical analysis of the ash of the leaf reveals the fact that a considerable proportion of it is composed of silica. Between the two epidermal layers of the leaf (Fig. 73) is the mesophyll (M), composed in part of parenchyma containing chlorophyll grains, and with intercellular spaces, and in part of parenchyma devoid of either chlorophyll grains or intercellular spaces; the former kind constitutes the bulk of the mesophyll, while the latter occurs as a bundle sheath surrounding the

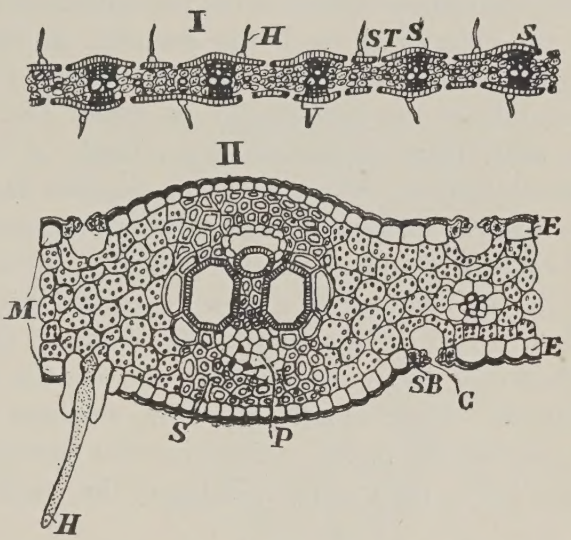


FIG. 73. I. A transverse section across part of the leaf of *Zea Mais*, magnified about 80 times. II. A small portion of I, magnified 300 times. E=epidermis; G=guard-cell; H=hair; M=mesophyll; P=phloem. The xylem is the group of large vessels seen immediately above the phloem. S=sclerenchyma; SB=subsidiary cell; ST=stoma; V=vascular bundle.

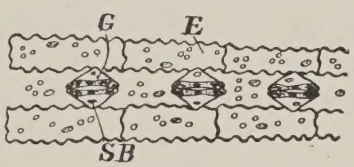


FIG. 74. A piece of the epidermis of the leaf of *Zea Mais* stripped off and examined in surface view. Magnified 300 times. E=epidermal cell; G=guard-cell; SB=subsidiary cell.

vascular bundles, and as groups of cells beneath the epidermis, and especially well developed in the region of the midrib.

The intercellular spaces of the mesophyll are in direct communication with the exterior through the stomata, so that there can be a free interchange of gases. The vascular bundles (V) run approximately in the middle of the mesophyll; on either side of them, i. e. between them and either epidermis, are strands of strengthening tissue or sclerenchyma (S), which with the bundles form complete bridges of rigid material passing from epidermis to epidermis; it is thus that the long leaf is supported and prevented from bending sharply upon itself by the leverage of its own extended mass. The main bundles in their structure are similar to those of the stem, but the finer ramifications are much reduced, and consist only of a few tracheids or vessels. Each bundle, even the smallest one, is surrounded by an endodermis; in the main veins this consists of a lignified parenchyma, but in the others, of ordinary thin-walled parenchyma.

(C.) The Root.

In its main features the minute structure of the root of a monocotyledon is similar to that of a dicotyledon, though differing from it in a few important details. If we examine a section across any part of the root of a *Zea Mais*, we shall find that it is the same whether the section is taken through the base or just behind the apex; but in the case of a dicotyledon, like that of the bean or sunflower root, for instance, we have seen that the structure of it in these two regions is very different, owing in part to the formation of cork and the consequent disappearance of the cortex, and in part to the secondary thickening formed by the cambium. In the root of *Zea Mais* there is neither secondary thickening nor cork-formation, and the root once formed undergoes no alteration.

Externally (Fig. 75, P.L) the root is limited by a single layer of cells from which the root-hairs (RH) arise, and which may be called the **piliferous layer.** It is not homologous to the epidermis of the root of the dicotyledon but to the outer layer of the cortex of that, for reasons which we shall consider when studying the apical development of the monocotyledonous root (infra, p. 116). Within the piliferous layer is a broad zone of parenchyma (COR) with intercellular spaces, constituting the **cortex.** The innermost layer of this (EN) consists of uniformly arranged cells, with the characteristic dot on their radial walls, surrounding the vascular strands; this is the

endodermis. Within the endodermis is a layer of parenchyma not quite so uniform in arrangement, laden with starch granules, and which constitutes the **pericycle** (PR), or inner one of the two investing layers of the stele. Within the stele is the intra-stelar tissue composed of parenchyma (P), and embedded in which are many (12–15) **protoxylem strands** (PX), with the large vessels of the later-formed primary xylem at the centre. Alternating with the protoxylem strands are those of the **primary phloem** (PP). The stele of the monocotyledonous root thus differs from that of the dicotyledon, in the large number of its vascular strands; for we have seen that in the latter class the stele of the root is **tetrarch**, i. e. contains only four protoxylem strands, whereas in the former it is **polyarch**, or contains many vascular strands. As a rule, we shall find that the number will be some multiple of three, i. e. nine, twelve, fifteen, or more.

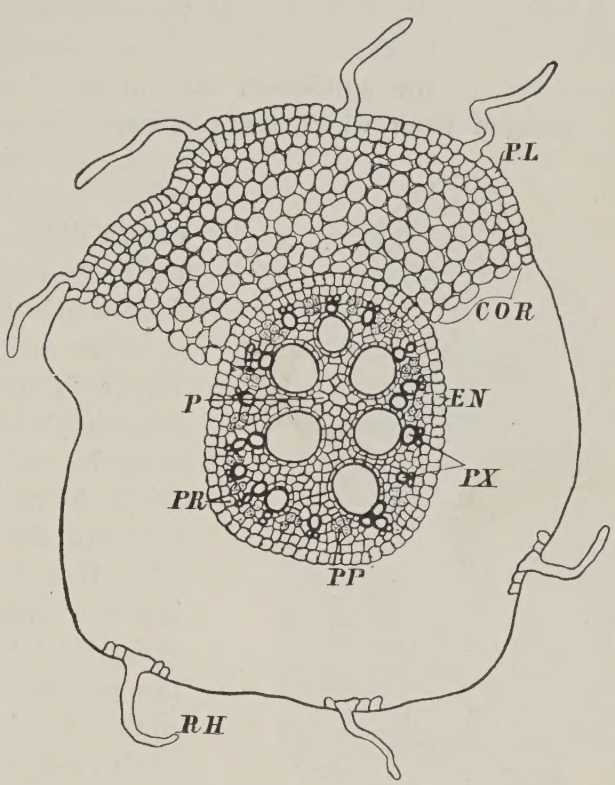


FIG. 75. Transverse section across the root of *Zea Mais* in the root-hair bearing region. Magnified 300 times. Only a portion of the cortex (COR) and piliferous layer has been represented. COR=cortex (extra-stelar tissue); EN=endodermis; P=pith; P.L=piliferous layer; PP=primary phloem; PR=pericycle; PX=protoxylem. The big vessels within these are the remaining portions of the primary xylem. RH=root hair.

(D.) APICAL DEVELOPMENT.

(*a.*) THE SHOOT.

The growth of the stem at its apex in *Zea Mais* is essentially the same as that in the sunflower (supra, p. 72) and so need not be re-described.

(*b.*) The Root.

Unlike the stem, the apical development of the root in the dicotyledon and monocotyledon, though the same in its general plan, differs in one important detail which we must now consider. At the apex of the root in the sunflower, and in most dicotyledons, there is a calyptrogen from which the root-cap arises, a dermatogen which forms the epidermis, and a portion of the apical meristem which becomes differentiated into an outer periblem and a central plerome, from which the cortex and vascular cylinder are respectively derived. But in the root of *Zea Mais*, as in monocotyledons generally, the layer (Fig. 76, OC) which at first sight might be mistaken for the dermatogen of the dicotyledonous root, when traced upwards to the apex is seen to arise from the same apical group (AC) of meristem cells as the periblem or cortex (C) itself, so that this layer is shown from its mode of development to be simply the outermost layer of the cortex, and is not, therefore, homologous to the epidermis of the dicotyledon, which arises from a distinctly separate layer of its own.

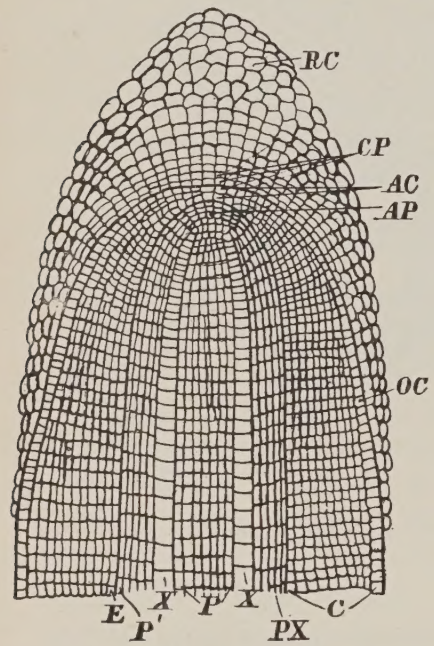


Fig. 76. Median longitudinal section through the apex of the root of *Zea Mais*. Magnified 300 times. AC=apical group of cells from which the periblem and piliferous layer arise; AP=apical group from which the plerome arises; C=cortex; CP=calyptrogen; E=endodermis; OC=outer layer of cortex (piliferous layer); P=pith; P′=pericycle; PX=cells which become primary xylem; RC=root cap; X=cells which become differentiated into the protoxylem.

In the axis of the root is a clearly defined **plerome-cylinder**, which can be traced upwards to a group of meristem cells (AP) continuous with the group AC, though for diagrammatic purposes it has been represented in the figure as somewhat too clearly demarcated from that. The outermost layer of the plerome-cylinder when traced downwards is found to become continuous with the pericycle, while the layers of cells next within this become continuous with the primary phloem and primary xylem; the strands of large cells marked X become continuous with the large vessels of the primary xylem, which

lie centrally to the smaller vessels of the protoxylem strands (Fig. 75). The central tissue of the plerome-cylinder becomes the pith (intra-stelar tissue). Outside the periblem, at the apex of the root, is a formative layer, the **calyptrogen** (Fig. 76, CP), the cells of which divide by periclinal walls, and from which the root-cap (RC) is derived.

Thus the monocotyledonous root develops at its apex in much the same way as that of the dicotyledon; there is a common apical meristem from which the plerome and periblem become differentiated, and a calyptrogen which gives rise to the root-cap. The only difference is in the absence of a distinctive dermatogen, so that the monocotyledonous root does not possess a true epidermis, but a differentiated outer cortical layer.

The supporting roots that grow out from the stem above the ground differ from the ordinary ones just described, in that the outer layers of the cortex, the endodermis, and the intra-stelar tissue surrounding the primary xylem strands become lignified, and therefore renders them very rigid, so that they are able to afford considerable support to the stem.

CHAPTER VI

ARBOREOUS TERRESTRIAL TYPE

ADAM'S NEEDLE (*Yucca*).

1. External Characters.

Yucca is a tropical arboreous representative of the lily family, which has become very generally cultivated in the gardens and greenhouses of this country. It possesses, in the plants more commonly seen, a stem of about one to two feet in length, though in older plants it is considerably longer. It is bigger at the base than at the apex, and so has an elongated slightly conical form. At the summit of the stem a crown of very long, stiff leaves of a dark green colour are borne, and over the surface of the stem, the closely packed scars indicating the places of attachment of past leaves can be seen.

The root is a fibrous one, consisting of a large number of fibres arising from the base of the stem.

The plant flowers but very seldom; the flower-stalk arises in the axil of one of the uppermost leaves and reaches a length of some three or four feet. Along its upper two-thirds are borne the flowers, arranged on short stalks with the youngest at the top and the oldest at the base; the inflorescence is thus a raceme (cp. p. 299). Each flower is pale pink in colour, and consists of a perianth of six divisions and inferior in position. The stamens are six in number, and the gynæcium is syncarpous, and composed of three carpels. The flower in fact is of the typical liliaceous kind (infra, p. 350).

From our point of view, *Yucca* is interesting since it shows the exceptional feature of secondary thickening in a monocotyledonous stem, so we will now proceed to study the minute structure of it.

2. Internal Structure.

The Stem.

In the older portions of the stem of *Yucca*, there are to be found two kinds of bundles: **cauline** (C.B′) and **common bundles** (C.B). The latter we have already studied in other plants, for they are those which are common to leaf and stem; in *Yucca* they run the same course and have the same disposition as those in a palm stem, or in the apical region of the maize stem. The cauline bundles, on the other hand, lie peripherally to these, and occur in a ring-like zone in the circumferential portion of the stem; they are more numerous in the basal portion, and are absent in the apical region; and they are confined exclusively to the stem, and have no connexion with the leaves, hence their name.

In a transverse section of the stem made some way below the apex, we shall find that it is limited by a well-defined epidermis (Fig. 77, E), the outer and inner walls of the cells of which are suberized. Immediately within the epidermis are several layers of squarish or oblong cells, the walls of which are also suberized (C.C); this forms the corky layer, and it differs from the same layer that we have already studied in the dicotyledonous stem, in that it is directly derived by the suberization of the walls of ordinary parenchyma cells, and not by the formation of a cork cambium.

Within the cork, and occupying the central portion of the stem, is a thin-walled parenchyma (C.P), with intercellular spaces, forming a ground-tissue. In the apical region of the stem, vascular bundles (C.B) are to be found scattered throughout it, and here and there leaf-

trace bundles (L.T), passing outwards to the leaves. But in the lower portions of the stem, about six inches below the apex, a cortical ring of the ground-tissue shows merismatic characters, some of the cells beginning to divide. Lower still (Fig. 77 is a section through this region), a definite ring of cambium (C) is formed, and it can be seen that it is forming new cortical parenchyma on the outside and new vascular bundles and ground-tissue on the inside. In Fig. 77 the formation of a new bundle (B) within the cambium ring can be clearly seen; it arises by the division of the daughter-cells derived from the cambial mother-cell, and by the elongation and subsequent differentiation of these cells new phloem and xylem are formed. But the bundles thus formed differ from the bundles formed by the apical meristem, in that they are cauline (C.B′) and not common bundles (C.B), i. e. they are confined to the stem, and do not pass outwards to the leaves.

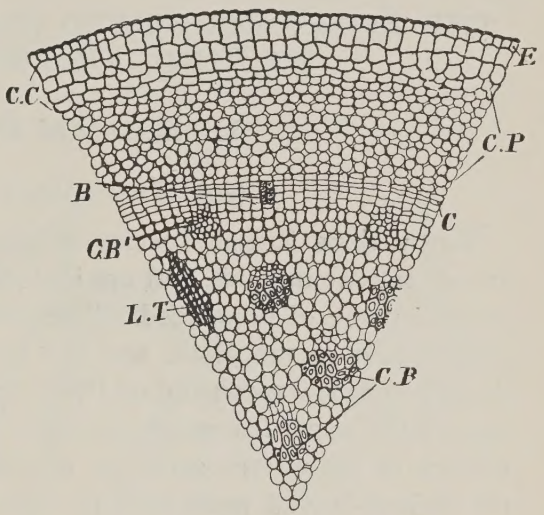


FIG. 77. Portion of a transverse section through the stem of the Adam's Needle (*Yucca*), near the base. Magnified 300 times. B=bundle in course of formation by the cambium; C=cambium; C B=common bundles; C.B′=cauline bundles; C C=cork cells; C.P=cortical parenchyma; E=epidermis; L.T=leaf-trace bundles cut across obliquely.

The stem of *Yucca* can thus increase year by year by the addition of new tissue, so that the basal or older part of the stem is thicker than the apical or younger parts. It is exceptional among monocotyledons in virtue of this secondary thickening of the stem, which differs, however, from that in dicotyledons, in that the whole of the vascular bundle is formed from the inner side of the cambial ring, and not xylem on the one side and phloem on the other.

Dracæna, the dragon's tree, is also an exceptional monocotyledon in that its stem becomes secondarily thickened, in the same way as that of *Yucca*.

CHAPTER VII

AQUATIC TYPE

THE BROAD PONDWEED (*Potamogeton natans*) and THE SHINING PONDWEED (*P. lucens*).

1. External Characters.

(A.) The Shoot and Root.

The various British species of *Potamogeton*, some ten in number, are all aquatic in habit, and are included under the very comprehensive popular name of pondweed. They are to be found scattered over the greater part of the globe, and are mostly inhabitants of fresh water, though some few species adapt themselves to salt water. In some British species the upper leaves are borne on long leaf-stalks, and float at the surface of the water; such are the broad pondweed (*P. natans*), and the various-leaved pondweed (*P. heterophyllus*), while all the others, including the shining pondweed, have all their leaves submerged and stalkless. In the broad pondweed the floating leaves are traversed by several longitudinal nerves, are oblong or ovate in form, thick and opaque in texture, and vary from two to four inches in length; the submerged leaves vary in their form, some consisting of a narrow, thin lamina, with a stalk, while others are devoid of the lamina and consist of nothing but the stalk. In the axils of both the floating and submerged leaves are thin membranous stipules (Fig. 78, s), which ensheath the stem, and are often an inch or slightly more in length. In the shining pondweed (*P. lucens*) (Fig. 78), the leaves are usually all submerged, though exceptionally a few float on the surface. They are all thin and sessile (stalkless), broadly lance-shaped in form, tapering at both ends, and may vary from two to six inches in length, though seldom more than half an inch broad at their broadest part; each leaf is traversed with a well-marked midrib, and on either side of this are two or three longitudinal veins, connected by transverse connexions, with a tendency, here and there, to form a reticulation. As in the broad pondweed, each leaf bears in its axil an elongated, thin, membranous stipule (Fig. 78, s). In other species, such as the fennel pondweed (*P. pectinatus*), the stem-sheathing axillary stipules

above described are either wholly absent or occur but rarely, and are replaced by a membranous expansion of the base of the leaf.

The stem is very elongated, floating and forked, and arises from a perennial root-stock which lies buried in the mud at the bottom of the water. From the root-stock, numerous fibrous roots arise, and spread downwards through the mud.

(B.) The Flower and Fruit.

The flowers are very small, and are closely crowded on the upper part of a fleshy axis of about two inches in length (Fig. 78, FA and F).

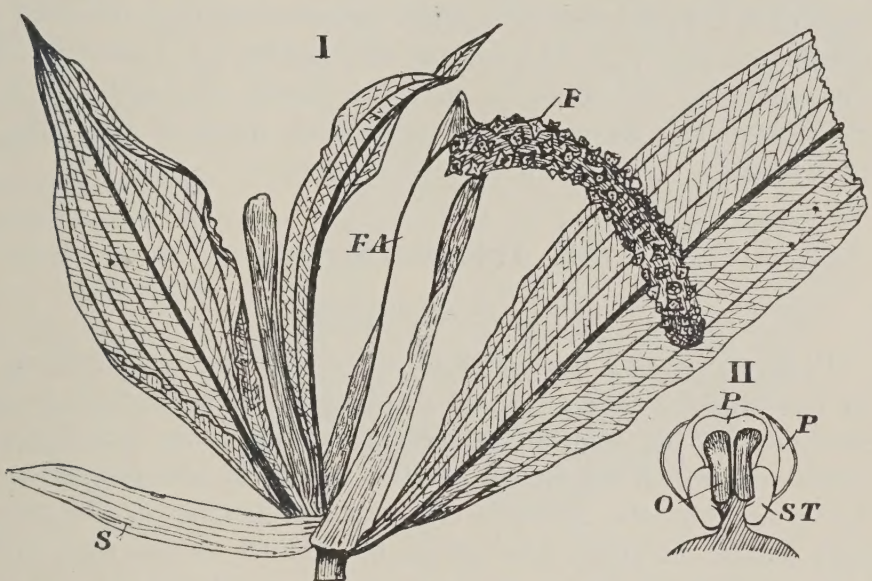


FIG. 78. I. The floral spike and leaves of *Potamogeton lucens* (Shining Pondweed). II. Vertical section of a single flower. F=a single flower of the spike; FA=floral axis; O=carpel; P=leaf-like outgrowths of stamens=perianth leaves of some authors; S=stipule; ST=stamen.

Each flower (F) is sessile (not stalked), and consists of four stamens and four carpels. The stamens (ST) are only shortly stalked, and from the connective, which joins the two anther lobes, there arises a scale-like appendage (P), regarded by some botanists as a perianth leaf. The gynæcium is apocarpous and consists of four carpels (O), each with a rounded stigma and no distinct style, and containing but a single cavity with one ovule. The arrangement of the parts of the flower in four, is not usual for monocotyledons, it as a rule being in three or some multiple of three in nearly all orders of the class, the arrangement in 2, 4, or 5 being comparatively rare. The parallel

venation of the leaf, the course of the bundles in the submerged rhizome, and the single cotyledon in the seedling plant are, however, all characteristic features of the class.

The fruits when ripe are small nuts, and the seeds are specially characterized by the absence of albumin (endosperm). The absence of this nutritive tissue seems to be a constant character in the seeds of all aquatic monocotyledons, and it is the more peculiar, because the ripe seeds of nearly all terrestrial monocotyledons are characterized by the relatively great quantity of endosperm which they contain. Doubtless the aquatic habit, which is possibly favourable to the easy possession of food-material and to rapid assimilation, renders the presence in the seed of a nutritive tissue unnecessary, and that which is present in the ovule before it ripens therefore becomes absorbed by the developing embryo. This may or may not be the correct interpretation, but the fact remains that the seeds of nearly all aquatic monocotyledons have no endosperm, while those of terrestrial habit have much.

2. Internal Structure.

(A.) Stem.

Examination of a transverse section across one of the floating stems of *Potamogeton natans* (broad pondweed) will show that the minute structure of the stem of this plant exhibits those typically aquatic characters which we studied in the petiole of the water-lily. The epidermis, and the immediately subjacent portion of the cortex, is very similar in either case (Figs. 65 and 66, E and O.C), and they differ in that in *Potamogeton* the outer cortical part, instead of consisting of five or six layers of cells, is composed of two layers only. The remaining portion of the ground-tissue is almost identical in either plant, consisting (Figs. 66 and 79) of trabeculæ of thin-walled parenchyma (TP), with the resulting large air-chambers (AC) so characteristic of all plants with an aquatic habit. The internal hairs so well developed in the water-lily are not present in *Potamogeton.* In the water-lily the vascular strands are arranged in two concentric rings, but in *Potamogeton* they are aggregated in the centre of the stem. This, however, is not an important difference, and is not a distinguishing one between the two classes of monocotyledons and dicotyledons, since in *Hippuris*, as we have seen, the vascular strands are aggregated in the centre of the stem as in *Potamogeton.*

The stele in *Potamogeton* (Fig. 79) is limited externally by a well-marked **endodermis** (EN), the inner wall of its constituent cells being very much thickened and lignified, and exhibiting distinct stratification; in iodine-stained preparations it can be seen to be crowded with starch granules. The radial walls also show the characteristic dot, due to a wavy folding of the wall in the vertical direction. The **pericycle** (P) is composed of a single layer of parenchymatous cells fairly uniform in size and arrangement, and containing starch granules. Within this is the **intra-stelar tissue** (IT), composed of polygonally-shaped parenchyma cells, crowded with large chlorophyll granules. The vascular bundles which are embedded in this, are very clearly seen on account of the large tubular cavity which traverses each one. In essential features, they are structurally similar to those of the water-lily, consisting of a large tubular vessel (Fig. 79, U, M, L, and C), the wall of which is composed of a single layer of small-celled parenchyma with unlignified cell-walls. To the central side of some of the vessels, there is, however, a strand (W) of very small but elongated cells with thickened and lignified walls, which serve to give support to them. Upon the outer side of some of the vessels and surrounding others is the phloem, consisting of large sieve-tubes (S) each of which is surrounded by a

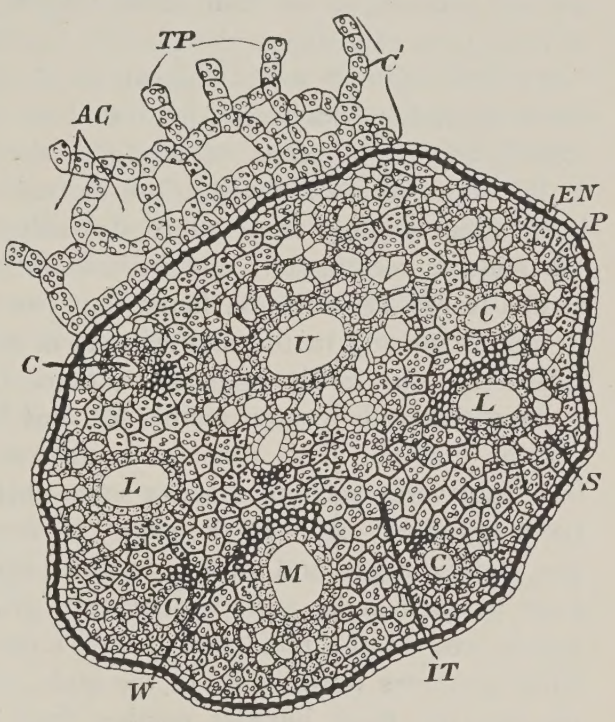


FIG. 79. The central portion of a transverse section across a floating stem of *Potamogeton natans* (Broad Pondweed). AC=air-chambers; C=cauline bundles; C'=inner portion of cortex; EN=endodermis; IT=intra-stelar tissue; L=the two lateral bundles coming in from the leaf at the first node above the plane of section; M=the median bundle coming in from the leaf at the first node above the plane of section; P=pericycle; S=sieve-tubes; TP=trabecular tissue; U=the united trace of the median and lateral bundles coming in from the leaf at the second higher node above the plane of section; W=sclerenchyma.

small-celled parenchyma with dense protoplasmic contents. The vascular bundles are thus much reduced, and contain no true xylem vessels; this condition, as we have seen (supra, p. 102), is the same as that in the water-lily, and is one which is characteristic of all wholly aquatic stems; those stems, like that of *Hippuris*, for instance, which are not submerged for their whole length, possess a certain quantity of true xylem elements in the vascular bundles.

At first sight it might appear as if the vascular bundles were indiscriminately scattered in the intra-stelar tissue, but careful examination of a series of sections, shows that the arrangement is the same for all sections taken through or near a node, and that these differ slightly from internodal sections. Roughly the form of the stele is rectangular, and in internodal sections, like that represented in Fig. 79, it will be found that two bundles (U and M) always lie approximately in the shorter axis of the rectangle, and that two others (L, L) lie in the longer axis; at each of the four corners of the rectangle there is a small bundle (C), and here and there, a few others may be present. This constant arrangement of the bundles as seen in a transverse section depends upon their constant course through the longitudinal extent of the stem; for from each leaf, three bundles, one slightly larger and median and two smaller and lateral, enter the stem at each node, and passing very gradually inwards run downwards, and at the node next below unite to form a single bundle. This continues downwards in the stele, and at the next lower node receives the three bundles coming from the leaf at the node next above, and so on for the whole length of the stem. In any internodal section, therefore, the united trace (Fig. 79, U) of the bundles coming from the second higher leaf will be seen, as well as the still separated median (M) and lateral bundles (L and L) of the leaf of the next immediate node above the plane of the section. The cauline bundles (C) (bundles which are confined to the stem and do not run out into the leaves) will occupy the same place in the section at any level.

The stem of *Potamogeton natans* thus not only represents a typical aquatic condition, but like that of the arboreous monocotyledonous stem of *Dracæna*, it serves also as an example of a stem with cauline bundles.

CHAPTER VIII

MINUTE STRUCTURE OF FLOWER OF ANGIOSPERMS

We have already seen (supra, pp. 12, 22) reasons for regarding the flower as a modified shoot in which the internodes are suppressed and some of the leaves are adapted to bear the reproductive bodies. We must now study the minuter structural features of the flower, in the course of which we shall seek for other evidence bearing upon this theory of the evolution of the flower. The study of the detailed structure of the flower involves three stages of inquiry: i.e. its development; its structure at the stage when it is ripe for the act of fertilization; and the nature of the changes subsequent to that, and which are collectively comprised under the term of embryology.

(A.) Development of Flower (*Inula Helenium*).

The development of the flower can be best studied in one of the *Compositæ* where there are a large number of florets (little flowers) of different ages crowded together on a flattened receptacle; it is thus possible by making a median vertical section through the floral head and examining it under the microscope, to trace various stages of development in the same section, since in the composite floral head the florets in the centre are the youngest and those on the circumference the oldest. If we examine a very young head of such a plant as *Inula*, or the sunflower, each floret will be seen to arise as a papilla-like outgrowth of periblem from the floral head (Fig. 80, I and II, P), into which a vascular strand (V) projects. A little later, the apex of this papilla ceases growing, and the growth is continued by a ring of matter round the circumference of its summit (Fig. 80, P′); this ring is the rudiment of the corolla, and soon after its formation it is prolonged upwards into five papillæ, of which three (Fig. 80, III) appear first, and the other two slightly later. These papillæ are the fundaments (rudiments) of the petals. The whole corolla continues its growth as a tube with the five papillæ at its summit; while the tube is still very short, five other papillæ (IV, S) appear on its inner surface at its base; these later become the

stamens. From the summit of the floret within the ring of stamens, there is formed a tubular depression (IV), and later from either side of this a papilla next arises (V, ST); by subsequent growth the two papillæ become carried together and fuse, except at their apex, to form the style. These two papillæ, together with the depression, are the fundaments of two carpels, and at first they are quite free, so that the gynæcium is apocarpous[1], the syncarpous condition not arising until later. The cavity formed by the depression enlarges to form the ovary (O) and from the base of this an ovule (OV) arises later.

The flowers of the *Compositæ* are somewhat exceptional in that the sepals (IV, C) do not arise until after the petals; they arise from the

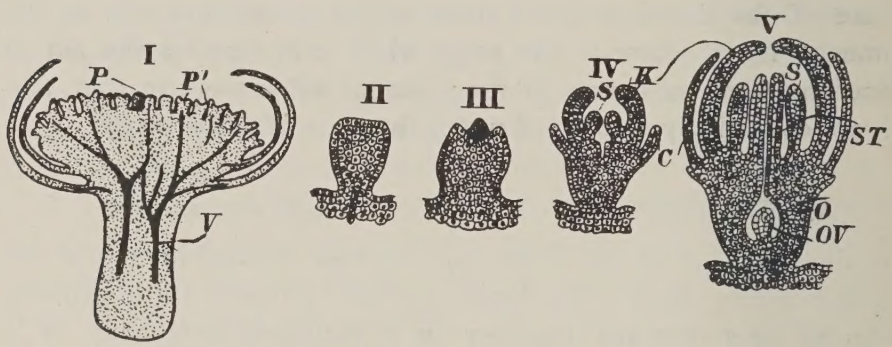


FIG. 80. I. A median vertical section through the young flower-head of a Composite flower, Elecampane (*Inula Helenium*), showing the developing florets. P=rudiment of a floret; P'=later and more advanced rudiments; V=vascular bundles. II. The early rudiment P in I, magnified 300 times, and showing it to consist of a papilla of periblem tissue covered externally with dermatogen. III. A more advanced rudiment showing three papillæ which are the rudiments of petals. IV. A more advanced stage. C=sepals; K=corolla (petals); S=stamens. V. A still more advanced stage, in which all parts of the flower are present. O=ovary; OV=ovule; ST=style. Other letters as in IV.

floral papilla, a little below the base of the petals and on their outer surfaces about the same time that the stamens appear. In most flowers the sepals appear first, then the petals, stamens, and carpels in order. Their later appearance in the flowers of *Compositæ* is probably due to the specialized condition which these have attained; for in most flowers of this order, the calyx consists of hairy filaments known as a pappus, and in some it does not appear until the fruit is formed. If we except then the exceptional condition of the flower of the *Compositæ*, we see that the floral organs arise in the same order as leaves, i.e. in acropetal succession, and that their mode of origin as papilla-like outgrowths of the dermatogen and immediately subjacent

[1] For definition of apocarpous and syncarpous cp. p. 291.

layers of the periblem, is identical with that of leaves. Thus the facts of development support the conclusion which we had previously arrived at from a comparative study of the fully formed flower. And the conclusion that the flower is a modified vegetative shoot is not so remarkable as it might at first sight appear, for among some of the lower plants—the vascular cryptogams for instance—the reproductive bodies are borne upon leaves which differ not at all, or but little, from the ordinary foliage leaves. When we come to study the fern and *Selaginella*, we shall see definite examples of this; in the common male shield-fern the reproductive organs are borne upon the under surface of any of the foliage leaves, and those which bear the reproductive spores in no way differ from those which do not. But there are other ferns, *Lomaria* and *Osmunda* for instance, in which the upper leaflets are much reduced in their vegetative structure and bear the reproductive bodies, and stages in this reduction may be traced from the lower unmodified leaflets to the upper modified ones. In the gymnosperms, as we shall see when considering *Pinus*, the flowers still retain a very obvious leaf-like character. The reproductive bodies are thus outgrowths from the surface of foliage leaves, which in most instances are modified to a greater or less degree.

We must now consider the further development of the different whorls of the flower, and in doing so it will only be necessary to confine our attention to the androecium and gynæcium, since the sepals and petals develop like ordinary leaves.

(B.) Further Development of the Androecium.

At the stage when we left the developing stamens, each one consists of a little papilla arising from the axis of the floret at the base of the developing petal tube. If we examine a transverse section across the stamen at this stage, it will present a somewhat oval-rectangular outline (Fig. 81, I), and will be limited externally by a single layer of dermatogen cells (E), enclosing a central mass of periblem parenchyma. It is therefore at this stage decidedly leaf-like in structure. A little later some of the periblem cells immediately beneath the dermatogen, at each of the four corners of the anther, divide up by walls parallel to the surface (periclinal walls) and produce four strands of actively dividing cells running the whole length of the anther (A, A). Each of these strands is called an **archesporium**, because from them the male reproductive bodies or **micro-**

spores—in angiosperms and gymnosperms called **pollen grains**—arise. The archesporium continues to divide and soon gives rise to a column of large cells (Fig. 81, II, A), with plentiful protoplasm and large nuclei, and at the same time some of the periblem cells outside the archesporium divide and form three or four layers of cells around it (T). The cells of the innermost of these layers then elongate radially and form a well-marked wall around each archesporium, called the **tapetum**. The function of this layer is to nourish the developing pollen grains, and at first its cells are rich in protoplasm. After the archesporial cells have divided for some time, division then ceases, but the anther as a whole goes on growing, and the cells separate slightly from each other and become somewhat rounded in

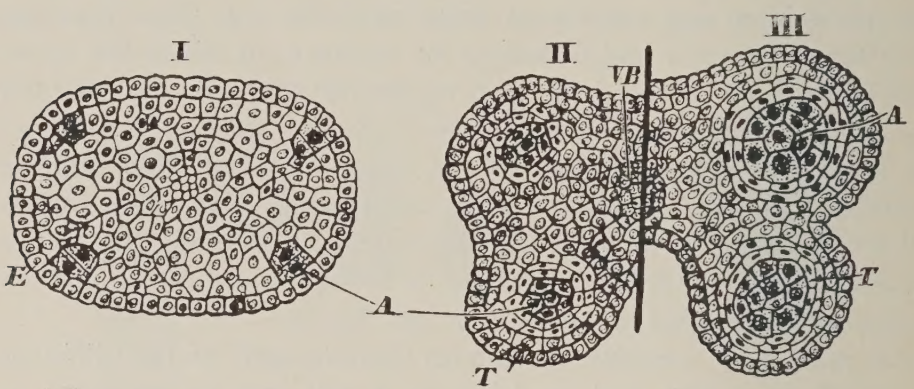


FIG. 81. Successive stages in the development of the anther of *Fritillaria*. I. Transverse section of a very young anther. A = archesporium; E = dermatogen. II. A slightly later stage. A = dividing archesporium; VB = vascular bundle. III. Still later (pollen mother-cell) stage. A = dividing archesporial cells; T = tapetum.

form. Each cell at this stage is called a **pollen mother-cell** (Fig. 82, P.C) because from each of them four pollen grains are formed.

The nucleus of each pollen mother-cell divides into two (Fig. 82, I), and each of these two divide again (II); cell-walls later appear between the nuclei so that the pollen mother-cell now contains four cells, which are so arranged that three lie in one plane, and the remaining one in another (III), or, in other words, each one lies at the angle of a tetrahedron. These cells are the **pollen grains**, and soon after their formation they are liberated by the dissolution of the wall of the mother-cell. While these changes are going on, the cell-walls of the tapetal cells disorganize, and their protoplasm is liberated into the cavity containing the pollen grains; these latter complete their growth by absorbing the tapetal protoplasm.

The anther itself during the formation of the pollen grains undergoes alteration in form and becomes constricted into two lobes (Fig. 82), united by a central isthmus of tissue, called the **connective**, along the axis of which a vascular bundle (V.B) is developed. In each lobe are the four cavities containing the pollen mother-cells and which are called the **pollen-sacs**. Soon after the formation of the

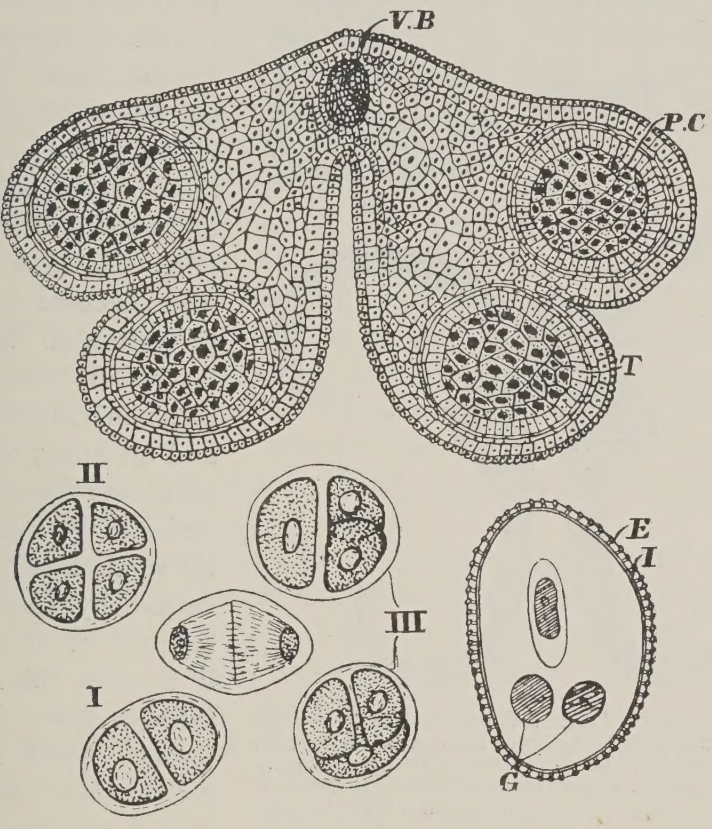


FIG. 82. The top figure represents a transverse section across an anther of the Lily at the pollen mother-cell stage. P.C=pollen mother-cells; T=tapetum; V.B=vascular bundle. I. A pollen mother-cell divided into two. II. One divided into four. III. Arrangement of the four cells into the form of a tetrahedron. The central figure of this group shows the nuclear spindle which is formed in the course of mitotic division. The figure on the right-hand side of the group shows a ripe pollen grain. E=extine; G=generative nuclei; I=intine. The large oval body within the grain is the vegetative nucleus.

pollen grains from the pollen mother-cells, the septum (Fig. 82) which divides the two pollen-sacs of either lobe, breaks down, so that each lobe then contains but a single sac (Fig. 83). Concurrently with these changes, the cell-walls of the cells lining the pollen-sacs undergo suberization, and assume a very characteristic fibrous appearance, and form a layer of tissue to which the name of **fibrous layer** is applied

(Fig. 83, FL). This layer is instrumental in the dehiscence or breaking open of the pollen-sacs, and at the point (D) where it joins the septum that originally divided the pollen-sac into two, it is extremely thin. It is at this point that the anther breaks open, the rupture being the result of a tension set up by the drying and consequent contraction of the fibrous layer.

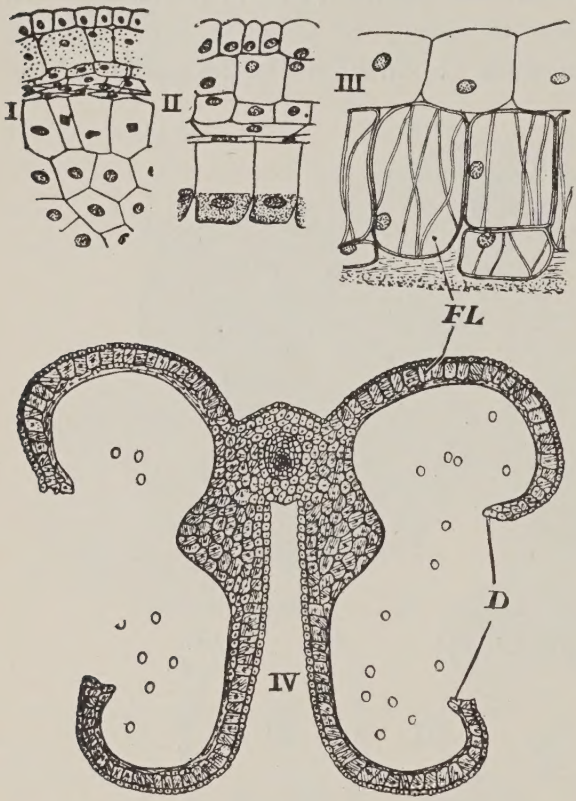


FIG. 83. Anther of Lily. I. A portion of a transverse section of an anther at the stage represented in Fig. 82, to show the details of the wall of the pollen-sac. Passing from without (upper surface) to within there is shown in order, the single-layered epidermis, then a layer of large cells which become later the fibrous layer FL, then three layers of small cells called the 'transitory layer,' and then the layer of large cells constituting the tapetum. The polygonal cells within this are the pollen mother-cells. II. A later stage; the tapetum beginning to disorganize. III. A portion of the wall of the ripened pollen-sac, magnified 300 times. The tapetum and the transitory layer have disappeared, and the walls of the large cells are suberized, and form the fibrous layer FL. IV. A transverse section of a ripe anther. D=line of dehiscence; FL=fibrous layer. A few pollen grains are represented in the cavity of the pollen-sac.

The pollen grains contained in the pollen-sacs are round or oval in form (Fig. 82, E) and their walls become thick and differentiated into two layers: an outer, thicker, cuticularized **extine** (E), and an inner, very thin, cellulose **intine** (I). The extine may be perforated by small holes, or traversed by depressions, so that at these parts it is very thin. It is through these holes or thinned areas that the pollen-tubes are protruded at a later period. At first, the pollen grain contains a single nucleus, but this divides into two (Fig. 82), and one of these then divides again, to form the two **generative nuclei** (G). There are thus present in a ripe pollen grain, three nuclei, i. e. the two generative nuclei and the large vegetative one, and around them the protoplasm of the grain aggregates. The pollen grain is now ripe and ready to pollinate the female portion of another flower. The

act of pollination will be better understood if we defer its study until we have considered the development and structure of the ovule.

(C.) Further Development of the Gynæcium.

Shortly after the rudiments of the carpels appear, a thickened ridge arises on the inner surface of each of their two margins, and it is from these ridges that the ovules arise; each ridge is known as a placenta. The number of rudiments which appear is equivalent to the number of carpels, so that in a monocarpellary ovary there is one, in a bicarpellary ovary two, and in a tricarpellary ovary three rudiments, and so on. In an apocarpous gynæcium these rudiments remain free, and each gives rise to a separate carpel, but in a syncarpous gynæcium they either early fuse together, or, after the rudimentary papilla are formed, continue their growth basally as a common tube. Septa may be next formed and divide this common tube into a number of compartments equal to the number of carpels present, or it may remain single chambered. The number of placentæ that develop on the inner surface of the tube or on the inner angles of its united septa, are a pair for each carpel, one along each margin of the carpellary rudiment (Fig. 84, I).

The carpels, like the stamens, petals, and sepals, thus arise like leaves, and the placentæ are thickened tracts developed along their margins, upon which later the ovules develop. Hence we often speak of the carpels as carpellary leaves, and we shall see that they are homologous with the carpellary scales of *Pinus* and the sporophylls of *Selaginella* and the fern. In fact they differ from these, mainly in that they have bent upon themselves, and so confine the ovules in a closed box. That this conclusion is a correct one, is further shown by comparing the developing stages of the ovules of angiosperms and gymnosperms with each other and with the corresponding stages in the development of the sporangia of *Selaginella* and the fern.

Development of the ovule. The ovules arise (Fig. 84, I, o), like the pollen-sacs, from groups of merismatic cells, in part derived from the epidermis—at this stage really an active dermatogen—and in part from the periblem of the developing carpellary leaf, the groups being arranged in a line along the placentæ. As the cells of each group divide they form a papilla-like eminence (Fig. 84, I, o), which grows out from the placenta, into the cavity of the ovary. As soon

as this outgrowth reaches a certain size, one of the cells (I and II, A) in the middle line, immediately underneath the epidermis, grows much bigger than the others, and is further distinguished by its abundant protoplasm and large nucleus; this cell is the **archesporial cell**, and the rest of the tissue in which it lies is the **nucellus** (N). In most instances, the archesporium soon after its formation divides by the formation of two transverse walls into three cells. Of these, the two upper ones (those nearer the epidermis) wither up, and finally disappear, while the lowest of the three continues to grow, and eventually becomes the **embryo-sac** of the ovule (III and IV). In some instances, in the lily and *Fritillaria* for example, and in other monocotyledons and some few dicotyledons, the archesporial cell does not divide, but becomes the embryo-sac directly.

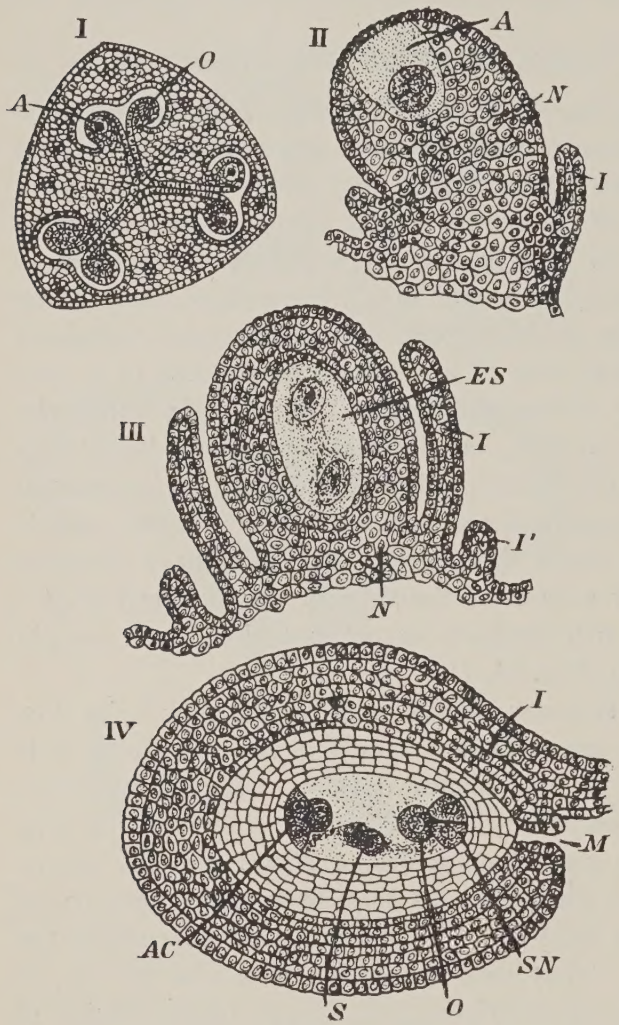


FIG. 84. Successive stages in the development of the ovule. I. Transverse section of a young ovary of *Fritillaria*. A=archesporium; O=developing ovule. II. A developing ovule, magnified 300 times. A=archesporium; I=developing inner integument; N=nucellus. III. A later stage. ES=embryo-sac at a stage when its nucleus has divided into two; I=inner integument; I'=developing outer integument; N=nucellus. IV. A mature ovule of Marsh Marigold. AC=the three antipodal cells; I=inner integument; M=micropyle; O=ovum; S=secondary nucleus; SN=synergidæ. The mass of cells surrounding the embryo-sac is the nucellus.

While these changes are taking place within the group of merismatic cells, there arises from around the base of the developing

ovule, a ring-like ridge of tissue (Fig. 84, II, I) which gradually grows upwards over the whole, and becomes the **inner integument** of the ovule. Soon after its formation, a similar ridge (I′) arises outside it, and at the base of the ovule, and in the same manner grows upwards and invests the ovule in a second or **outer integument.** The two integuments thus formed completely enclose the **nucellus** or original outgrowth, except that at the apex they do not close in but leave a narrow aperture, called the **micropyle** (IV, M). In dicotyledons and a few monocotyledons, the two integuments contribute to the formation of the lips of the micropyle, but in most monocotyledons the inner one alone forms the micropyle, the outer one stopping short in its growth, and so not reaching as far as the aperture formed by the inner integument. If the student will compare the development of the integument in the ovule of *Pinus* (infra, p. 156), which is taken as a type of a gymnosperm, with that here described for angiosperms, he will see that in the former only one integument is formed ; and if he will carry this comparison farther, and compare the development of the sporangium of cryptogams (*Selaginella* and the fern), it will be evident that it differs from that of the phanerogam ovule, in that the bud-like outgrowth (nucellus) does not become invested in any integument at all. In fact the integument of the ovule of the phanerogams or flowering plants is a new structure, *sui generis*, which in the evolution of plants appeared first in gymnosperms as a single-layered, and later in angiosperms as a double-layered investment. It thus follows that the nucellus of the phanerogam ovule is the homologue (agreeing in anatomical relations and mode of development) of the cryptogam sporangium. Hence, cryptogams never develop seeds like phanerogams, since the seed is the ripened ovule, of which the integuments become the seed-coats.

Returning now to the embryo-sac, we find that it grows rapidly, and in most instances absorbs the cells of the nucellus (Fig. 84, III, N), so that it comes in contact with the inner integument. In other instances, as in the lily and *Fritillaria*, the nucellus remains until fertilization, and in some cases even persists until the germination of the seed ; in this latter case, the persistent nucellus is known as the **perisperm,** and serves as a source of nutriment for the growing embryo. While the embryo-sac is growing, its nucleus divides into two (Fig. 84, III, ES), and each of the daughter-nuclei travels one to either pole of the sac. Each then divides again, and almost immediately afterwards each of the four divides again, so that at both ends of the embryo-sac there

are four nuclei (IV), which at first are free, lying in the protoplasm of the cell. Subsequently three of these nuclei at either end become surrounded by protoplasm which is constricted off from the rest of the protoplasm, so that the nuclei become converted into cells. Of the two groups of three cells, that at the micropyle end of the embryo-sac is called the **egg-apparatus**, of which the two cells lying at the apex of the sac are the **synergidæ** (SN), and the one behind them, the **ovum** or **egg-cell** (O). The cells of the other group, lying at the opposite end of the sac, are called the **antipodal cells**, and probably represent a vestigial remnant of the cryptogamic prothallus. So far as is known, they play no part in the economy of the ovule and quickly disappear. The two nuclei, called the **polar nuclei**—one in either group—which do not become surrounded by a special investment of protoplasm, undergo a remarkable migration; for each of them advances towards the middle of the embryo-sac, where they meet and coalesce to form the **secondary nucleus** of the embryo-sac (IV, S). Shortly afterwards the synergidæ and ovum become much bigger. The ovule is now mature or ripe for the act of fertilization. We see then that the structure of the ripe ovule is as follows (Fig. 84, IV): externally it is invested in two membranes or integuments which are pierced at one end by an aperture, the micropyle; within the integument a nucellus may be present, but in a large number of instances it is much reduced or completely absorbed; within this is the embryo-sac with its contents, i.e. the egg apparatus, the antipodal cells, and the secondary nucleus. We shall see later (infra, pp. 158 and 176) that the synergidæ probably represent the last vestiges of an archegonium, an organ which is very characteristic of the higher cryptogams, and that the antipodal cells, together with the secondary nucleus, represent a reduced prothallus, an organ which in ferns is a sexual and independent plant, leading a separate existence, but which in the course of the evolution of the angiosperms has become reduced to a mere appendage of the spore-bearing plant.

(D.) Pollination and Fertilization.

We must now return to the anther. We saw that when ripe the pollen-sacs of the anther split open or dehisce and liberate the pollen grains (Fig. 83); these usually adhere to the open lips of the pollen-sacs and form easily detachable powdery masses on the surface of the pollen-lobes. The pollen represents the male and the ovules

the female portion of the flower, and it is necessary, before the egg within the latter can undergo further development, for it to be fertilized by fusion with some of the contents of the pollen grain. It is thus necessary for the pollen of one flower to be brought into contact with the female portion of another flower, and in angiosperms this may be done either by the agency of insects or of the wind. Owing to the fact that the ovules of angiosperms are enclosed within an ovary, the pollen cannot be deposited directly upon the ovules as in gymnosperms, but instead is placed by the insect or blown by the wind upon the stigma of the gynæcium. The various mechanisms by means of which the pollen is thus deposited are described in Part II, chapter XVIII, p. 306. The act of depositing the pollen upon the stigma of the flower, or as in gymnosperms directly upon the micropyle of the ovule, is known as **pollination**, and must be carefully distinguished from the final act, or that of **fertilization**. The stigma secretes a sugary solution, which serves, in conjunction with the glandular hairs that secrete it, not only to make the pollen grains adhere to the stigma, but also to nourish them, as a result of which they grow. Their growth consists in the formation of a long tube, called the **pollen-tube**, which grows through the soft tissue of the stigma and style into the cavity of the ovary. The pollen-tube is formed by the pushing out of the intine through one of the perforations, or by its bursting through at one of the thinned areas of the extine. In most instances the pollen-tube has to work its way through the loose tissue of the style, but in some cases, as in the pansy and the rhododendron, the style is perforated along its length by one (pansy) or more (rhododendron) canals, called **stylar canals**, along which the pollen-tube travels into the cavity of the ovary. It then travels along the wall of the ovary, usually along the placenta, until it comes within a certain distance of the micropyle of some one of the ovules, when it turns aside from its original course and grows towards and through the micropyle, until it reaches the embryo-sac. In some few cases, as in the alder-tree, the pollen-tube travels through the funicle and chalaza of the ovule to reach the embryo-sac. As soon as the pollen-tube is formed, the two generative nuclei are carried into it with the protoplasm, and throughout the subsequent growth of the tube they are lodged in its extremity. The vegetative nucleus soon disappears, and plays no further part in the economy of the pollen grain or tube. When the extremity of the pollen-tube reaches the embryo-sac, one or both of the generative nuclei pass out, and one of

the two continues its journey between the synergidæ, and ultimately reaches the ovum. It penetrates the protoplasm of the ovum, and finally fuses with its nucleus. Throughout the animal and plant kingdom alike, the essential act of sexual reproduction is the fusion of the male and female nuclei; this act is called **fertilization**. The results of fertilization are far-reaching, for the ovary becomes converted into the fruit, the ovule into the seed, and the fertilized ovum, called the **oospore**, into an embryo plant. The most important of these processes is the development of the embryo, for the other two are dependent upon and subservient to this.

(E.) Development of the Embryo.

The embryo plant arises from the oospore by its segmentation into a number of cells from which the rudiments of the young plant are fashioned and the primary tissues, i.e. dermatogen, periblem, and plerome, take their origin. The embryos of monocotyledons and dicotyledons exhibit certain important differences in their mode of development, which are constant for the two classes. We will therefore study them separately, commencing with that of the dicotyledon.

(*a.*) Dicotyledonous Embryo (shepherd's purse).

The different stages in the development of the embryo may be easily observed in one of the commonest weeds, the shepherd's purse (*Capsella Bursa-pastoris*). At any time of the year, from spring to late autumn, this plant may be found in fruit, each fruit consisting of a triangular sac containing four rows of seeds. Any individual plant will contain the fruits in nearly all stages of development, the lower fruits being the most advanced and the upper ones the least. To examine the embryo, it is only necessary to break open the fruit and extract the seeds, and with two needles to slit these open on a glass slide in a drop of water, when the embryo will be liberated. In the very early stages the seed may be clarified (rendered transparent) by treatment with 5 per cent. acetic acid or with chloral hydrate, when the embryo can be seen *in situ*, or sections may be made of the seed, or a large number may be simply crushed and the chances taken of one of them showing a liberated embryo undamaged.

The first change that results from fertilization is the formation of a cell-wall round the oospore. Its nucleus then divides into two, which subsequently separate. The division of the nucleus is followed by that of

the cell, which divides by a transverse wall into two. Repeated transverse divisions then take place with concurrent growth, until there is formed a structure like that represented in Fig. 85, I; this consists of a number of cells arranged in a row, the two terminal ones of which are larger than the rest. Of these terminal cells, the lower one (that nearest the micropyle) is very large, and is called the **basal cell** (B), while the upper one is more or less spherical in form, and is called the **embryonic cell** (E). The whole structure at this stage is called the **pro-embryo.** Of it, only a small part is concerned in the formation of the embryo, for the embryonic cell contributes everything to the formation of the embryo, except the root-cap and the periblem of the root. The remaining portion of the pro-embryo, called the **suspensor,** merely acts as an organ of suspension, and in part as a source of nutriment for the embryo. The embryonic cell divides by three walls at right angles to each other, two longitudinal and one transverse, into eight cells or octants. Each octant then divides by a wall parallel to its outer surface into an inner and an outer portion (Fig. 85, II). The outer portion of the eight octants then divides by anticlinal walls (at right angles to the surface) alone, so that the embryo becomes invested in a single layer of cells the **dermatogen** (D); from this layer the epidermis of the plant is formed. The inner portions of the eight octants of the embryo divide into a central and an outer portion, which form respectively the plerome (P) and periblem (PL). The root-cap and periblem of the root are formed from one half of the last cell of the suspensor; this cell (Fig. 85, II, A) divides by a transverse wall into two, and the daughter-cell next the embryo by further divisions contributes to the formation of the root to the extent just indicated (Fig. 85, III, RC and PR). The plerome of the root is derived from the same source as that of the stem.

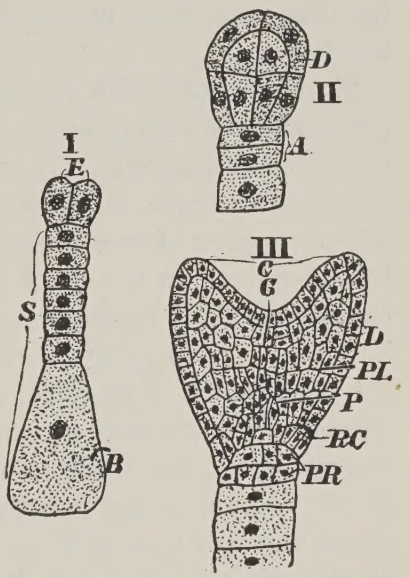


FIG. 85. Successive stages in the development of the embryo in the embryo-sac of the Shepherd's Purse (*Capsella Bursa-pastoris*). I. B=basal cell; E=embryonic cells; S=suspensor. II. A=the two cells derived from the division of the last cell of the suspensor; D=dermatogen. III. C=cotyledons; D=dermatogen; G=growing point of stem; P=plerome; PL=periblem; PR=periblem of root, derived from the upper one of the two cells marked A in II; RC=root-cap.

In its very early stages the embryo is spherical in form, but as growth proceeds it becomes flattened at the top and sides, and then two wing-like outgrowths (III, C) arise at its end, converting it into a heart-shaped structure. These two outgrowths are the rudiments of the cotyledons (seedling leaves), and between them is the growing point of the stem. In dicotyledons there are always two cotyledons, and they are *lateral* in position; the apex of the stem is constantly terminal and axial in position—that is, it lies in the same axis as the root.

Simultaneously with the progress of the changes just enumerated, the secondary nucleus of the embryo-sac gives rise to a nutritive tissue, called the **endosperm**. The nucleus divides and subdivides repeatedly, and fills the whole of the embryo-sac not occupied by the pro-embryo with a number of free nuclei, which subsequently become surrounded by cell-walls. In the shepherd's purse and a great many other plants the whole of the endosperm is absorbed by the time that the embryo is formed, but in others the endosperm is abundant and persists until the germination of the seed, when it is absorbed by the seedling plant. Seeds which contain no endosperm are entirely occupied by the embryo plant, and are known as **ex-albuminous seeds**; while those which contain it are usually filled mostly by it, the embryo being small, and are known as **albuminous seeds.** Familiar instances of ex-albuminous seeds are those of the bean-plant, pea-plant, wall-flower, sunflower, lupine, maple, cucumber, &c.; instances of albuminous seeds are those of *Zea Mais* (Indian corn)—which is in reality a special kind of fruit—coffee-plant, date, castor-oil plant, elder-tree, &c.

(*b.*) Monocotyledonous Embryo (water plantain).

A very convenient plant for purposes of studying the development of the embryo in monocotyledons is the water plantain (*Alisma Plantago*). The oospore divides by two transverse walls into three cells arranged in a row (Fig. 86, I, C, SR, B). Of these cells, two take part in the formation of the embryo, while the lowest cell (B), that nearest the micropyle, becomes very large and does not contribute to the embryo. The uppermost cell divides by a vertical wall into two (II, C), and these two by a transverse wall into four (III, C); this group of cells, instead of giving rise, as in the dicotyledon, to nearly all the embryo, here only forms the single cotyledon or seedling leaf. The

middle cell (I, SR) divides by several transverse walls, to form a group of cells (II, S & R) of great importance. The cells of this group divide by vertical walls (III, S & R), and the cells of one side of the group S give rise to the stem, while the whole of the group R ultimately form the root. The next cell-divisions are confined to the group marked C (IV), and as the result of which the cotyledon becomes very large. Later, however, the other groups divide, but the group marked S far less numerously than either of the other two. After a great many cell-divisions have taken place, the embryo attains the form indicated in V, where the cotyledon (C) is by far the most important organ in respect of size, while the radicle (young root) (R) is about half its size,

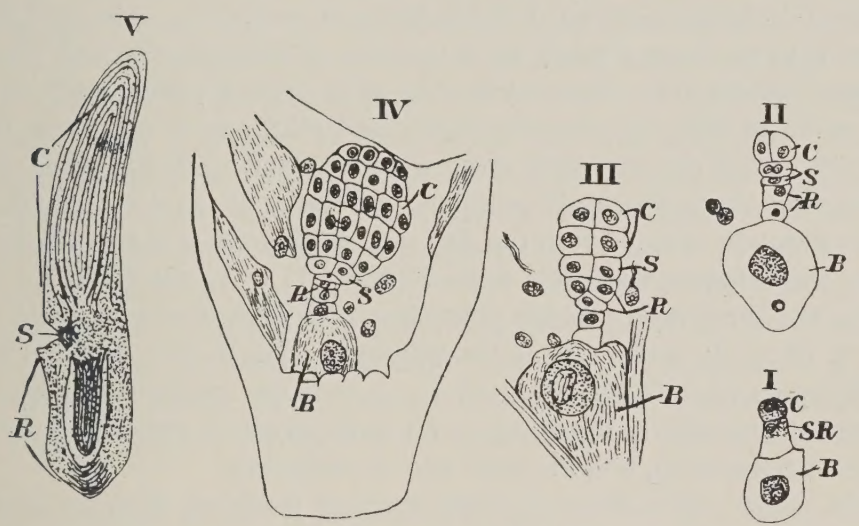


FIG. 86. Successive stages in the development of the embryo of the Water Plantain (*Alisma Plantago*). B = basal cell; C = cotyledon; R = root; S = stem; SR = cell from which stem and root are derived. In I, II, III, and V the embryo alone is shown, but in IV, part of the embryo-sac and a few cells of the endosperm are represented.

and the stem (S) is exceedingly small and hidden in a depression at the junction of cotyledon and root. The monocotyledonous embryo is thus characterized by the following characters, in respect of which it is strongly contrasted to that of the dicotyledon: the cotyledon is single and axial, lying in the same axis as the root, while the stem is lateral in position. These combined differences between the two classes are constant.

The endosperm is formed in the monocotyledon in very much the same manner that it is in the dicotyledon. In *Alisma Plantago*, however, it becomes absorbed before the embryo is fully formed; but in both classes the majority of plants have albuminous seeds.

(F.) The Ripe Seed and Fruit.

The principal result of fertilization is the formation of the embryo, but other changes also result, which are accessory to the main result, and which we must consider. The sum total of the changes produced by fertilization is the formation of the embryo and endosperm, the ripening of the ovule into the seed and of the ovary into the fruit. Both ovule and ovary undergo great enlargement, and their walls become more or less altered. The integuments of the ovule as a rule become denser and more decidedly membranous in texture, and in some cases (linseed) the outer integument becomes mucilaginous; the altered integuments are called the **testa** or seed-coat. The wall of the ovary, as we have already seen, consists of three layers, and when it ripens into the fruit, these layers may all become dry and woody, or one or more of them may become fleshy and juicy; as a rule those fruits which have a dry wall split open or dehisce and allow the seeds to fall out, while those which are succulent and fleshy do not dehisce. Hence fruits may be divided into the **dry** and **dehiscent**, and the **succulent** and **indehiscent** fruits (cp. chap. XIX, p. 317). In the dry fruits, as a rule, the three layers of the ovary lose their distinctness, and the wall as a whole is spoken of as the **pericarp**; but in the succulent fruits the layers retain their distinctness, so that the pericarp can be seen more or less clearly to consist of an outer layer or **epicarp**, a middle one or **mesocarp**, and an inner one or **endocarp**.

In some cases the accessory changes resulting from fertilization affect not only the ovule and the ovary, but other portions of the flower as well, and, as in the pineapple and fig, even the whole of the inflorescence may be involved. The strawberry and the apple are instances where the floral receptacle (thalamus) becomes succulent and enlarged, and contributes to what is popularly called the fruit. Botanically speaking, the fruit is the ripened ovary, and when other parts become involved in the changes that follow fertilization, the product is called a **pseudocarp** or false-fruit. The different kinds of seeds and fruits are described in chap. XIX.

CHAPTER IX

GYMNOSPERMS

SCOTCH FIR (*Pinus sylvestris*).

1. External Characters.

(A.) The Shoot and Root.

Pinus sylvestris, or the Scotch fir, is a tall tree, with evergreen needle-like leaves. Its habitat is essentially in high latitudes or altitudes; in this country it only occurs wild in Scotland, though it is much cultivated in the Southern Counties, especially in sandy regions. In the Scotch Highlands it may be found at an altitude of above 2,000 feet, while in the mountains of Southern Europe it occurs as high as 7,000 feet above the sea. It stretches in the form of vast forests across Siberia and Russia, extending into Prussia, Sweden, and Norway. Remains of it are found in the submerged forests and peat-bogs of Ireland, England, and Denmark, showing that in former times it spread over the lowlands of those countries. The group of plants (*Coniferæ*) to which *Pinus* belongs is of great geological antiquity, remains of it having been found in rocks of the Lower Cretaceous Age.

Examination of an individual tree shows that it consists of a vertically ascending, tapering main axis, from which lateral branches arranged in a whorl-like manner arise, tier after tier. And similarly, upon the lateral branches, other branches arise, arranged in a more or less whorl-like manner, each whorl being separated from those behind and in front by a considerable interval; in the older portions of the stem the whorls are approximately equidistant from each other. Examination of the terminal portion of one of the principal lateral axes, of such length that it shall contain three or four whorls of branches arising from it, will show that its apex is terminated by a **terminal bud**, immediately behind which there will be three or four **lateral buds**, and among these a more or less globular body, the surface of which is marked off into square areas (Fig. 87, I): this body is the young female flower, called a **female cone**, and a very superficial examination will show at once that it occupies the same position

as any of the lateral buds. The lateral buds are undeveloped shoots, and in the course of the year develop into a whorl of lateral branches with their leaves, in every respect identical with the successive whorls behind it. The terminal bud also develops and continues the main axis, and at the end of the year there will be found at the termination of the axis of the current year another terminal bud with lateral buds and a female cone, just behind it. Next year these develop in the same way; hence it follows that the interval between any two whorls of branches represents a year's growth, and therefore that the age of any lateral axis may be ascertained by counting the number of its whorls. We have already seen that the young female cone is borne near the extremity of the current year's shoot; at the extremity of the last year's shoot, i.e. among the first whorl of branches, there is a much larger cone, still green, and in its second year (Fig. 87, II). At the extremity of the shoot of the year before last, i.e. among the second whorl of lateral branches, there is a cone of about the same size as the second-year one, but brown and lignified, and with its constituent foliar scales separated slightly from each other; this is a three-year-old cone, and it contains the matured seeds, which at about this period fall out from it and are carried away by the wind.

The processes of pollination and fertilization in *Pinus* occupy a somewhat extended period; the small female cones of the current year contain the developing embryo-sac and the ovules become pollinated about the end of May; the cones of the second year become fertilized in the June of this year by the pollen deposited in the May of the preceding year, so that after the former month these cones contain a developing embryo which reaches maturity about September of the same year. The cones of the third year undergo an elongation of the floral axis, by means of which the floral scales are carried apart from each other, and the seeds, which are lodged upon their upper surfaces, are thus enabled to fall out.

We have seen that the female cones occupy the position of buds, and that buds are rudimentary shoots which later develop into full shoots. Hence we must regard the female cones as morphologically equivalent to a shoot of which the leaves have become modified for reproductive purposes. That this is so is further exemplified by the condition of some female cones of the larch which the author once noticed growing on some trees in a Devonshire lane. The axis of each of these cones is continued forwards beyond the

reproductive scales as a purely vegetative shoot identical with the ordinary vegetative shoots of the plant; so that the cone could be described as a vegetative shoot, the basal portion of which had become modified for purposes of reproduction.

The **male cones** occur on the same tree as the female, but on different branches. They are difficult to find in the earlier stages of their development, since they appear to be similar to an ordinary vegetative bud. If the scales which invest the bud be removed it will be found that lateral axes arise in their axils; and if various stages in the development of the bud be examined it will be seen that these axes do not all develop alike: some, those at the apical portion of the bud, become ordinary foliage shoots (Fig. 97, F), while those on the basal portion become modified and form the male cones (C). The male cones are therefore, like the female cones, modified shoots.

The younger lateral branches of the tree bear numerous foliage leaves which are of simple needle-like form. The leaves apparently arise from the lateral branches in pairs, but a careful examination shows that they do not arise directly from the lateral branches, but from the summit of a very small suppressed branch which is hidden by a number of small, brown, dry membranous scales, in the axil of one of which it arises: from their position upon the stem and the mode of their development these scales are morphologically equivalent to leaves, and are called **scale leaves**. Upon the older portions of the main stem and of the lateral branches leaves are absent, but the scars where the scale leaves and suppressed branches were once can always be seen. The suppressed branches and the leaves live for about two or three years and then fall off.

We can thus distinguish in *Pinus* two kinds of shoots, the vegetative and the reproductive, and in the former we can distinguish two kinds of stems and leaves. The stems whose axes are continued forward year by year, by means of the terminal or lateral buds, are **stems of unlimited growth**, while those which bear the green acicular leaves are **stems of limited growth**. The brown scarious scales are the **scale leaves**, and they perform no physiological part in the respiration or assimilation of the plant; the green needle-like leaves are the **foliage leaves**, and they perform the physiological activities of leaves.

In some gymnosperms (*Phyllocladus*) there are no foliage leaves, only scale leaves, and in this plant the shoots themselves become leaf-like in form and assume the function of leaves. In others, scale

leaves are absent and all the leaves are foliage ones; this is the case in the monkey puzzle (*Araucaria*), in the juniper tree (*Juniperus*), and in *Thuja*. In the spruce fir and the Irish yew scale and foliage leaves occur on the same shoots, but in this instance the scale leaves merely serve as a protective covering to the bud. In *Pinus*, as we have seen, both kinds of leaves are present, but the scale leaves are borne upon the shoots of unlimited growth, and the foliage leaves upon those of limited growth, which die and fall off in the course of about three years.

The root of *Pinus* is a tap-root, with its ramifications; like the stem it is continually thickening.

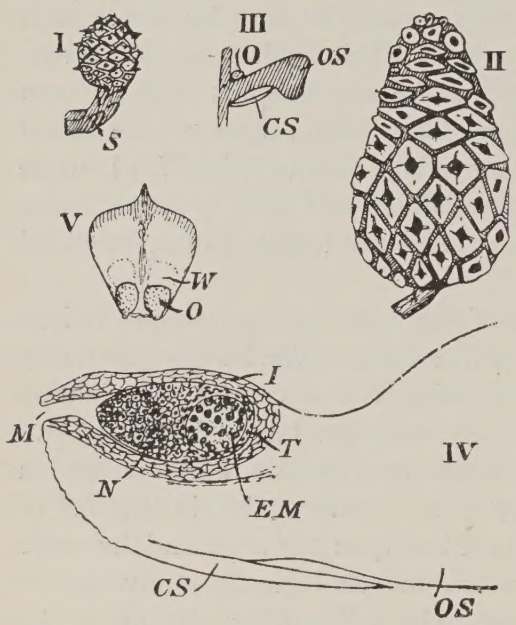


FIG. 87. I. A first-year female cone of *Pinus sylvestris*. II. A second-year cone. III. A median longitudinal section through an ovuliferous scale of the first-year cone. IV. A median longitudinal section through the ovule and part of the ovuliferous scale of the first-year cone. V. Upper surface-view of an ovuliferous scale from a first-year cone. I and II natural size; III and V enlarged 5 times; IV magnified 70 times. CS = carpellary scale; EM = embryo-sac; I = integument; M = micropyle; N = nucellus; O = ovule; OS = ovuliferous scale; S = scale leaves; T = tapetum; W = wing of ovule.

(B.) The Reproductive Organs.

The Female Cone. If we examine a first-year cone early in the year (Fig. 87, I), we shall find that at its base there are a number of scale leaves (S); in the axil of one of these the cone arises. The study of the gross structure of the cone, with which we are now alone concerned, is better pursued upon the second-year cone, which is much bigger. Its surface (Fig. 87, II) is marked off into rhomboidal areas, which follow a spiral course; each area is the thickened apex of an **ovuliferous scale**, and they are larger at the base than nearer the apex of the cone. Examination of the cut surface of a median, vertical section will show a central axis around which the ovuliferous scales are borne. By either carefully smoothing the surface of the section or by removing some of the ovuliferous scales it will be seen that the latter arise in the axils of very small brown scales (Fig. 87, III and IV, CS), morphologically equivalent to the scale leaves at the

base of the cone; these are called the **carpellary scales.** Upon the upper surface of each ovuliferous leaf (OS), at the end attached to the axis, are borne two **ovules** (V, O), which thus lie naked and unenclosed in an ovary. The absence of an enclosing ovary is one of the important distinctive features that distinguish the gymnospermous flower from that of the angiosperms; and hence in them there is no need for a style or stigma, since the pollen is deposited directly upon the micropyle of the ovule. The purpose of the ovary in the angiospermous flower, i. e. that of protecting the ovules, is attained in the gymnosperm by the contact of the ovuliferous scales over all the surface of the cone until the seed is ripened; for a short time only, about May 21st, are the scales slightly opened in the first-year cone, in order to allow the pollen dust to reach the ovule.

In *Pinus* the carpellary scale is very small, and in a second-year cone may be quite withered up, but in *Abies* (Fig. 88) it is persistent and is as long as the ovuliferous scale, so that it is easily seen at the surface of the intact cone. If now we imagine that the ovuliferous leaf could be reduced to a mere swelling upon the carpellary scale, and that this latter were to turn in its margins so as to form a closed box, we should have an arrangement very similar to that of the ovary of the angiospermous plant, in which the carpellary scale would represent the wall of the ovary, the ovuliferous scale the placenta, and the ovule is of course homologous in either case.

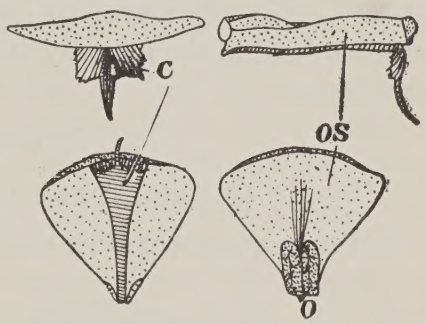


FIG. 88. The ovuliferous scale of *Abies* (one of the Firs). C=carpellary leaf; O=ovule; OS=ovuliferous scale.

Examination of an ovule (Fig. 87, V) of the second year will show that it consists of an ovoidal swollen part, the ovule proper (O), continued outwards into a wing-like membranous expansion (W); the wing, by presenting a comparatively large surface to the wind, enables the ovule to be carried a considerable distance from the parent tree. At the apex of the ovule, which is directed towards the axis of the cone, can be seen a relatively wide aperture, the **micropyle** (Fig. 87, IV, M), through which the pollen grains gain access to the egg-apparatus within.

The Male Cone. Like the female cone, the male cone consists of a central axis (Fig. 97, II, A) with the reproductive leaves (S)

arranged spirally round it. In the male cone these leaves are called **stamens** or **staminal leaves**, and each one consists of an expanded portion, the **anther** (Fig. 98, II, AN), attached to the axis by a short **filament**; the anther bears on its under surface two sacs, the **pollen-sacs** (P) or **microsporangia**, and within each sac is a yellow powder, the **pollen** or **microspores** (M).

The detailed structure of the reproductive organs will be studied later, but we may, before leaving the study of the gross structure, call attention to the fact that the reproductive leaves, i. e. carpellary scales and staminal leaves (stamens), are arranged upon the axis of the cone in the same way that the vegetative scale leaves are, i. e. in a spiral. The elongation of the floral axis and the arrangement of the leaves just described, is one of the characters that distinguishes the gymnosperm flower from that of the angiosperm; for in the latter the floral axis is much shortened, so that the floral leaves come to lie close together, and in the majority of cases they are arranged in whorls, not in spirals.

2. Internal Structure.

(A.) Minute Structure of the Stem.

In the arrangement of its internal tissues the stem of *Pinus* is similar to that of the arboreous dicotyledonous stem, though certain important differences of detail exist.

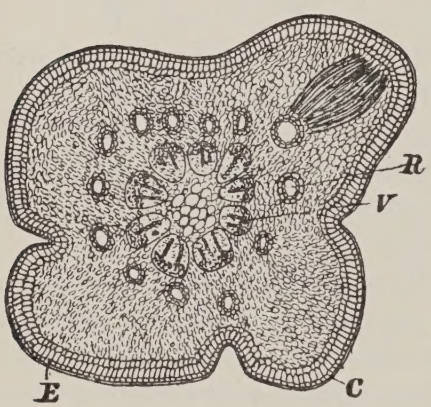


FIG. 89. A transverse section of the very young stem of *Pinus*, taken through the bud. C=cuticle; E=epidermis; R=resin passage; V=vascular bundle. The protuberance at the top right-hand corner is a branch of limited growth cut through very obliquely, and the dark mass in the middle is its vascular cylinder. Magnified 80 times.

The very young stem, that forming the axis of either a terminal or lateral bud, is fundamentally of the same structure as the younger portions of the sunflower stem, or that in the bud of the elm, and is monostelic. In section its outline is very irregular (Fig. 89), on account of the closely packed branches of limited growth which arise from it. On the outside it is limited by a fairly well defined epidermis (E), with thick outer walls and a cuticle (C). Within this is the extra-stelar ground-tissue or cortex, surrounding the vascular cylinder. The cortex con-

sists of parenchyma, the cells composing which have cellulose walls and intercellular spaces. The endodermis is not clearly differentiated and is difficult to observe. The pericycle consists of some six to eight layers of parenchymatous cells not differing in any marked manner from those of the cortex, except that the walls of the cells are somewhat thinner and the protoplasm slightly more granular; these differences disappear in the older portions of the stem. In the pericycle are a number of tubular resin passages (R), each lined by a definite epithelium, so that the pericycle is heterogeneous. The vascular bundles are not fused, but free; each is wedge-shaped, and consists of **primary xylem** with a centrally situated **protoxylem** of spiral and annular vessels, and an outwardly situated **primary phloem**; cambium is not yet definitely formed.

In an older portion of the stem—that of the current year—we shall find that many of the cells of the cortical parenchyma are dividing (Fig. 90, CR), in order to keep pace with the increase of the central tissues. Immediately below the epidermis and at the bases of the depressions formed by the irregular contour, there are strands of sclerenchyma. A little way within the epidermis, in the peripheral portion of the cortex, there is a band of **cork cells** (CK) arising from a **phellogen** (P), derived by tangential division of some of the cortical cells; the cork thus arises in the same way as that in the stem of the elm. The vascular bundles are larger than those in the bud-stem, since the rest of the primary xylem and phloem, and some secondary xylem and phloem, have in addition been formed by the cambium (C.A), which at this stage forms a well-defined layer of regularly arranged cells. An **interfascicular cambium** has formed in the parenchyma lying between the primary bundles in the same way as that in the sunflower or the elm stem; a small amount of interfascicular xylem and phloem has been formed by it, so that the bundles now constitute a continuous ring, interrupted only by the narrow primary medullary rays. The internal contour of the vascular ring is wavy, the crests of each wave marking the position of the primary bundles, at the apices of which are the protoxylem strands.

The cambium can be best studied at this stage; its cells are very regularly arranged in radial lines, its walls are very thin, its protoplasm copious, and one layer of cells is narrower than the others. This layer is the one containing the mother-cells (supra, p. 50), the others contain the daughter-cells; these latter can be traced by insensible gradations to the elements of the phloem on the outside and those

of the xylem on the inside. The form of the xylem elements (X) (tracheides) is very uniform, and since they undergo but slight alteration in form, their outline is approximately that of the cambial cells from which they are derived. At more or less regular intervals in the

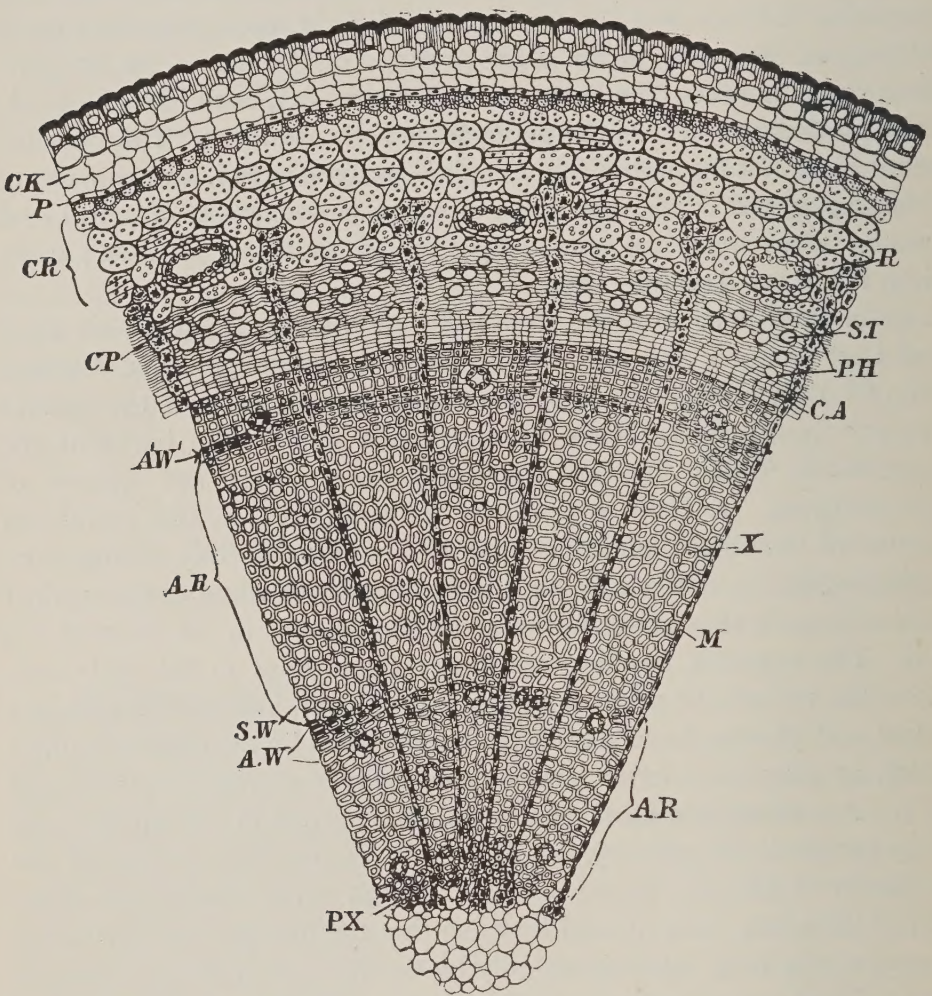


FIG. 90. A portion of a transverse section of a two-year-old stem of *Pinus sylvestris*. Magnified 300 times. AR=annual ring of first year; A.R=annual ring of second year; A.W=autumn wood of first year; A'W'=autumn wood of second year; C.A=cambium; CK=cork; CP=crushed phloem; CR=cortical parenchyma; M=medullary ray; P=phellogen; P.H=phloem; PX=primary xylem; R=resin passage; S.T=sieve-tube; X=xylem.

cambium ring, there are cells which have a greater radial diameter than others; these can be traced outwardly and inwardly into the medullary rays (M), so that these latter arise from the cambial cells.

The phloem (PH) consists of sieve-tubes and phloem parenchyma.

The sieve-tubes differ from those of the angiosperms, and resemble those of the vascular cryptogams in that the sieve-plates (Fig. 91, SP) are not deposited upon the transverse walls, but in groups upon the radial (lateral) walls only; companion cells are absent.

The xylem is composed exclusively of **tracheides**, in which respect it differs from that of the angiosperms and resembles that of the vascular cryptogams. Vessels are absent. The tracheides are prosenchymatous (Fig. 91, I and II, T) in form, with no protoplasmic contents, with lignified walls, and bordered pits arranged in a single line along

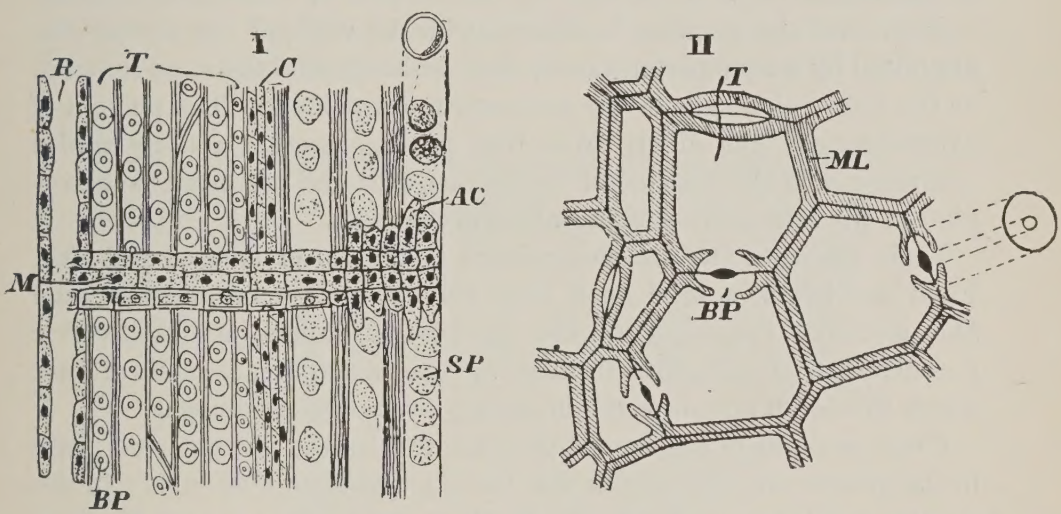


FIG. 91. I. A radial longitudinal section through the phloem and a portion of the xylem of the stem of *Pinus*. II. A small portion of the xylem of the stem of *Pinus* in transverse section. Both magnified 300 times, but II is drawn on a much larger scale. AC=albuminous cells; BP=bordered pit; C=cambium; M=medullary ray; ML=middle lamella; R=resin passage; SP=sieve-plate; T=tracheides.

the length of the cell and on the radial walls; the walls are also marked by a delicate system of two intersecting lines.

The medullary rays (Figs. 90 and 91, M), like those in the elm, are wall-like plates of cells, some of which pass through the vascular ring from the pith to the cortex, while others start at various depths in the xylem and end in the phloem: the first sort of rays are the **primary ones** and the others are the **secondary ones.** The character of the medullary rays varies with their position; that portion of each ray which traverses the xylem (Fig. 91, I, M) is composed of lignified cells with bordered pits and no protoplasm, together with cells possessing cellulose walls and plentiful protoplasm with starch and oil; the pits in the wall of the tracheides which abut on these latter cells are wider

than the others, thus indicating that they, which are themselves pitted by bordered pits opposite those of the tracheides, are physiologically connected with the tracheides in some important way. The portion of the ray which traverses the phloem is composed of cells with very plentiful protoplasm containing starch granules, prominent nuclei, and thin cellulose walls; in addition there are other cells (AC), elongated in the vertical direction and containing no starch; these are situated upon the upper and lower borders of each ray, and are also in opposition to the walls of the sieve-tubes. These cells are called the **albuminous cells** on account of the amount of proteids which they contain, and the surfaces in contact with the walls of the sieve-tubes are pitted by simple perforations; they probably fulfil the same function as the companion cells of the angiospermous phloem. The phloem of gymnosperms thus differs from that of angiosperms and resembles cryptogams, in the absence of companion cells and of transverse sieve-plates; the lateral sieve-plates alone are present.

Resin passages (R) are to be found in the cortex, xylem, and pith. Each consists of a tube lined by a definite epithelium or membrane and enclosed externally to this by several layers of small-celled parenchyma. Each arises from an intercellular space, the cells around which divide up and form the investing layers of the passage.

Older portions of the stem differ from that of the current year, only in the greater amount of cork and the absence of an epidermis; in the greater development of the xylem, which develops more quickly than the other tissues, and which in two-year-old and older stems (Fig. 90) shows the annual rings (A.R), composed of spring (S.W) and autumn (later) (A′W′) wood as in the elm, and in the larger number of secondary medullary rays. In three-year and older stems, the primary phloem and outer older layers of secondary phloem (CP) become crushed and distorted, owing to pressure produced by the continually increasing mass of the secondary xylem.

(B.) Minute Structure of the Foliage Leaf.

As seen in transverse section the outline of the leaf is semilunar, of which the flat side is morphologically the upper surface and the convex the lower. There is a well-defined epidermis (Figs. 92 and 93, EP), the cells of which possess thick cellulose walls, the outer ones being very thick and chemically altered upon their outer surfaces to form a thick cuticle (C). Along the whole length of the two margins of the leaf, at

the junction of the flat and convex surfaces, the outer wall of the epidermal cells is very much thicker than in the other cells, the result of which is to strengthen the leaf. The thick walls of the cells show very clearly a stratified structure, indicating that they have been thickened by the successive addition of new layers from within. The guard-cells (Fig. 93, GC) of the stomata lie in deep depressions of the epidermis; the epidermal cells bounding the stomata are radially elongated, and the stomal surface is protected with a cuticular layer continuous with that of the general surface. Immediately within the epidermis is a narrow band of tissue (H), some two layers in thickness, the cells of which along the margins of the leaf are larger than those within the general surface. This tissue is the **hypodermis**, and it is composed of cells with very

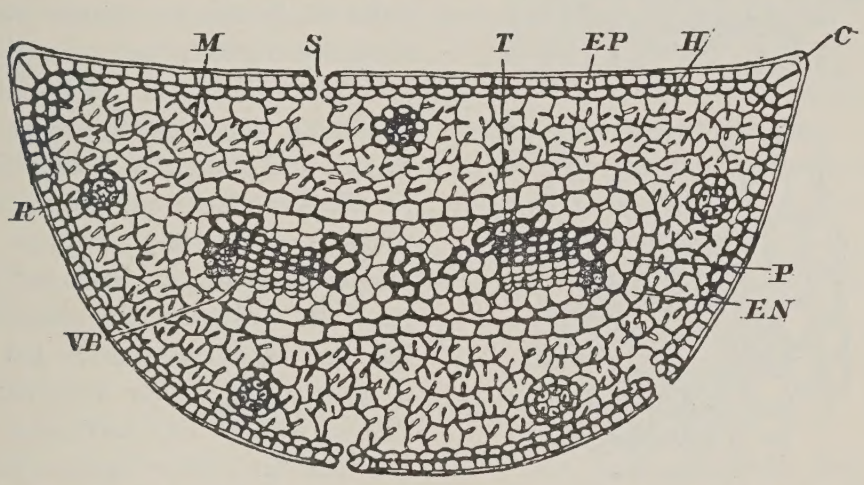


FIG. 92. Transverse section of the foliage leaf of *Pinus*. Magnified 300 times. C= cuticle; EN=endodermis; EP=epidermis; H=hypodermis; M=mesophyll; P=pericycle; R=resin-duct; S=stoma; T=transfusion tissue; VB=vascular bundle.

thick, simple-pitted lignified walls; so thick are the walls that the cavity of the cells is almost obliterated. In form the cells are prosenchymatous, and they are absent immediately beneath the stomata. The hypodermis is a strengthening tissue, and it is mainly to it that the rigidity of the leaf is due.

Within the hypodermis is the mesophyll (M), not differentiated into palisade and spongy parenchyma. It is composed of thin cellulose-walled cells, the walls of which are folded into the interior of the cells in a remarkable rosette-like manner; the protoplasm of the cells is crowded with chlorophyll granules, which are arranged as a layer upon the inner surfaces of the walls, and consequently follow the direction of the infoldings. What is the meaning of the peculiar infoldings

of the cell-walls? Owing to the form of the leaf, there cannot be contained within it a great quantity of mesophyll, the active assimilating tissue of the leaf, in consequence of which, were there no other provision made, the power of the plant to obtain its carbonaceous food would be very limited. It cannot provide for a greater quantity of this tissue by a general thickening of the leaf, because then the central portion would not receive sufficient light to develop chlorophyll, without which the leaf cannot assimilate; neither can it attain the desired end by the assumption of a flat, expanded, blade-like form of leaf, because in a plant with the habit of *Pinus*, the leaves would mutually obstruct the rays of light, and the power of assimilation would be consequently much reduced, and, moreover, *Pinus* lives in sandy and dry situations, and must consequently reduce its evaporating surface as much as possible. Hence the plant has but one other alternative left it: it must increase its assimilating surface without any corresponding increase in either size or bulk; obviously it attains this end by the infoldings of the walls of the mesophyll cells, for these increase the surface over which the chlorophyll grains of each cell may be spread, treble-fold or more, without increasing either the number or size of the cells. Arranged in the form of a broken ring, in the substance of the mesophyll, are resin passages (R), each lined internally with a thin-walled epithelium, and supported externally by a concentric layer of sclerenchyma.

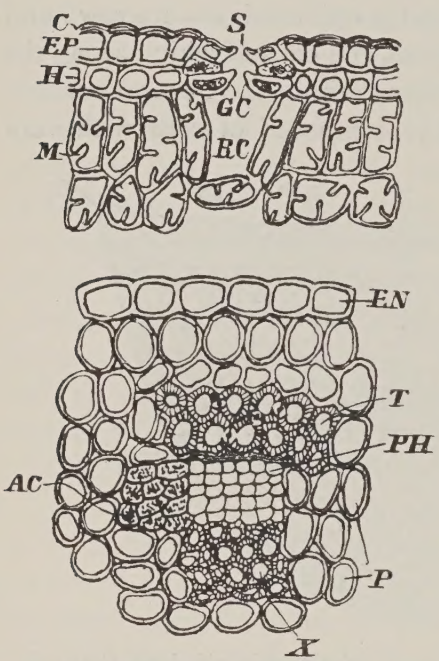


FIG. 93. The top figure represents a transverse section through a stoma of the leaf of *Pinus*. C=cuticle; EP=epidermis; GC=guard-cells; H=hypodermis; M=mesophyll; RC=respiratory chamber; S=stoma. The lower figure represents a transverse section through a vascular bundle and adjacent tissues in the leaf of *Pinus*. AC=albuminous cells; EN=endodermis; P=pericycle; PH=phloem; T=transfusion tissue; X=xylem.

In the centre of the mesophyll is a single layer of oval cells, forming a sheath oval in transverse section, called the **endodermis** (EN) or **bundle sheath**, the walls of which consist of cellulose, and are pitted by simple (tubular) pits. Within the endodermis

is the vascular cylinder, consisting of two centrally situated vascular bundles (VB), surrounded by a many-layered and differentiated **pericycle** (P). The vascular bundles are similar to those of the stem; the xylem is directed towards the upper surface of the leaf and cambium is absent. The pericycle consists of two kinds of tissue: externally, i. e. immediately within the endodermis, are parenchymatous cells with thin walls of cellulose and protoplasmic contents, and surrounding the vascular bundles within this, tracheides with lignified walls, bordered pits, and no cell contents. This latter tissue is called **transfusion tissue** (T), because it is thought that it conveys the water and dissolved mineral matter from the xylem through the other portion (parenchymatous) of the pericycle and the pitted endodermis to the mesophyll, and probably also the elaborated food-material from that to the phloem. At the angles of the phloem are a group of cells (AC), with thin cellulose walls and granular protoplasm; these are called **albuminous cells**, and doubtless are also of the nature of transfusion tissue.

The leaf of *Pinus* is thus one in which the tissues are arranged concentrically around the vascular bundles, and is therefore, like that of the stonecrop, of the **centric type**. The leaves of all gymnosperms are not of this type, however, for that of the yew (*Taxus baccata*) is distinctly **bifacial**.

(C.) Minute Structure of the Root.

The young root of *Pinus* (Fig. 94) in the main resembles that of a dicotyledon, but the cortex is not limited externally by a morphological epidermis, since, as we shall later learn, there is no dermatogen, or formative layer of the epidermis, at the apex of the root. It is at most a physiological epidermis, serving the same function as the epidermis of dicotyledons. Root-hairs, when present, are unicellular outgrowths of the outermost cells of the cortex; but they are not numerous, a fact which is doubtless correlated with the thickness of the cuticle of the leaves, with their small surface and consequent diminished numbers of stomata, and with the deeply-seated position of these latter; these are structural modifications which diminish the transpiration of water at the surfaces of the leaves, and consequently the amount required to be extracted from the soil.

The cortex (Fig. 94, C) is limited internally by a well-defined endodermis (EN), with corky walls and the characteristic dot on the radial ones. Within this is the pericycle (P), composed of three or four layers

of cells, of the ordinary parenchymatous kind. Centrally are the primary xylem (PX) and phloem masses, varying in number from three to four, and sometimes as many as six. In the main tap-root, the number of primary xylem strands is usually three (**triarch root**) and sometimes four (**tetrarch root**), but in the lateral roots it is usually two (**diarch root**). The primary phloem (PP) alternates with the xylem, so that the vascular bundle is of the radial type. The xylem masses lignify (Fig. 95) from without inwards, so that their development is centripetal like all roots, and the first part that is lignified in the elongating portion of the root is the protoxylem, composed of spirally-thickened tracheides.

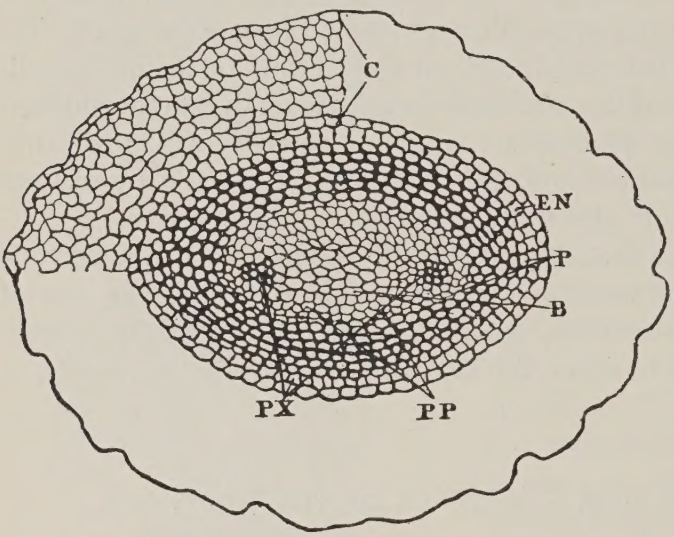


FIG. 94. Transverse section, just behind the apex, through the root of *Abies excelsa*. Magnified 300 times. B=pith; C=cortex (only a part represented); EN=endodermis; P=pericycle; PP=primary phloem; PX=primary xylem.

Within the vascular strands is a central pith (B) composed of parenchyma, which passes outwardly towards the pericycle between the phloem and xylem masses, forming the primary medullary rays.

In an older portion of the root, the cortical tissue and endodermis become disorganized owing to the development of a cork cambium from the outermost layer of the pericycle, and the consequent production of cork cells. Centrally to the pericycle, the parenchyma lying between the phloem and xylem divides to form a cambium (Fig. 95, CA), and from this arises secondary xylem and phloem (metaxylem and metaphloem respectively); the earlier formed secondary xylem occupies the interval between the primary strands. In a still older root the cortex disappears, and the periphery of the root is limited by a band of cork composed of many layers of cork cells, internal to which is the cork cambium. The phloem forms a complete ring, interrupted by narrow parenchymatous medullary rays; the primary

phloem, and in old roots the secondary phloem, becomes distorted and unrecognizable owing to the pressure produced by the development of the secondary xylem. The cambium forms a well-defined ring lying between the phloem and xylem; its characters are the same as that in the stem. The xylem also is in the form of a complete ring, interrupted only by the primary and secondary medullary rays, and, according to the age of the root, exhibiting two or more annual rings of the same structure as those in the stem. The primary xylem lies centrally on the internal margin of the secondary xylem as two, three, or more wedges which project into the very small pith, and which may be completely obliterated.

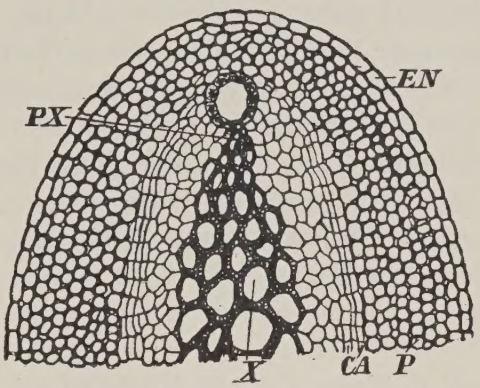


FIG. 95. A portion of a transverse section of an older root of *Abies excelsa*. CA=cambium; EN=endodermis; P=pericycle; PX=protoxylem; X=primary xylem. The primary phloem lies between the cambium and the primary xylem.

Lateral rootlets arise, very much as in the dicotyledonous root, from the pericycle; this is another feature in which the gymnosperms resemble the angiosperms and differ from the vascular cryptogams, in which the lateral rootlets arise, not from the pericycle but from the endodermis.

(D.) Growing Point of the Stem and Root.

(*a.*) Stem.

In its principal features the growing point of the stem of *Pinus* is similar to that of the sunflower, but the epidermis is not developed from a distinct dermatogen, since in *Pinus* that which corresponds to the dermatogen of the dicotyledon, i.e. the outermost layer of the apical meristem, gives origin not only to epidermis but also to a portion of the periblem, whence the cortex is derived. Moreover, at the apex, it is impossible to distinguish between the plerome and the periblem. In other words, the layers of the meristem are less distinct in gymnosperms than in angiosperms.

(*b.*) Root.

Like that of the stem, the main features of the apical development of the root are similar to those of the usual method followed in dicotyle-

dons, as illustrated by the sunflower root. But there is no dermatogen, and hence in the fully formed root no piliferous layer (epidermis) morphologically comparable to that of the dicotyledons. The periblem and plerome are distinct throughout; the latter gives origin to the central vascular cylinder, and the former to the cortical tissues, but also, by the division of the cells of its outermost, apical layer, to the root-cap. In very young roots, however, such as lateral roots which are just arising, there can be seen a differentiation of a calyptrogen from the periblem, which gives rise to the piliferous layer and root-cap. But this differentiation is soon lost, and at the apex of older roots it is not apparent, and the origin of the tissues is like that first described.

(E.) The Minute Structure of the Reproductive Organs.

(*a.*) The Female Cone.

We have already seen that the female cone consists of carpellary leaves with an ovuliferous scale arising in the axil of each, and that on the upper surface of each scale two ovules are borne (Figs. 87 and 88). We must now study the structure of the ovule in greater detail. If we examine an ovule of a first-year cone before June we shall find that it consists of a single integument (Fig. 87, IV, i) (not double as in angiosperms) within which is a parenchymatous tissue, with copious protoplasmic contents, called the nucellus (N); its micropylar end contains cells which are more granular than the remaining portion. Embedded in the nucellus near the bottom of the ovule is a large round sac, containing more or less numerous free nuclei; this is the **embryo-sac**, and the number of nuclei present in it depends upon the stage of development reached. The nuclei are not surrounded by cell-walls, but lie free in the protoplasm of the sac. This condition of the ovule is only a temporary one, for it represents but a stage in a somewhat slow development. Up to this stage, however, the development of the gymnospermous ovule is similar to that of the angiosperm, for in both classes it arises from a group of cells of the placenta[1], which, growing out, forms a little eminence of tissue, the nucellus. Within this one of the cells rapidly becomes larger

[1] The ovuliferous scale of the gymnosperm may be regarded as the morphological equivalent of the angiospermous placenta, since both arise from the carpellary leaf.

than the others, which continue dividing, while this one grows but does not divide for some time. This is the **archesporial cell**, and like the same cell in angiosperms it here also gives rise to the embryo-sac. When the archesporial cell reaches a certain size, it divides by a tangential wall into an upper slightly smaller cell and a lower larger one. The upper one divides up repeatedly and gives rise to a layer of tapetal cells (Fig. 87, T) which subsequently surround the embryo-sac (EM). The lower one divides into three cells, of which the two upper ones wither up and disappear, while the lowest one becomes the **embryo-sac** (EM). Thus the development of the gymnospermous ovule up to this stage differs from that of the angiosperm in the formation of a tapetum and in the non-development of an outer integument. But after the formation of the embryo-sac, development proceeds differently in angiosperms and gymnosperms. In the former group of plants its nucleus divides up and forms the egg-apparatus and antipodal cells, the endosperm developing after fertilization. In *Pinus* (as a type of gymnosperms), however, the nucleus of the embryo-sac divides up repeatedly and forms a large number of free nuclei (Fig. 87, IV, EM). At first these arrange themselves round the wall of the embryo-sac, but as they increase in number they invade the central part of the sac and ultimately fill it up. The embryo-sac grows rapidly and its nuclei divide and keep pace with its growth; as it grows it absorbs the nucellus, and ultimately it fills nearly the whole of the ovule, only a thin layer of nucellus persisting round it, and a conical mass at its micropylar end (Fig. 96, N). Cell-walls then appear between the free nuclei, so that the embryo-sac is filled with a thin-walled cellular tissue; this tissue is the **endosperm** or **prothallium** (Fig. 96, EN), and in gymnosperms it is formed before fertilization and not afterwards as in angiosperms. At about this stage certain of the cells of the endosperm, four or five in number, at the micropylar end of the embryo sac, become larger than the others, and further distinguished by their abundant protoplasm and large nuclei. These cells are the developing **archegonia** or **egg-apparatus** (Fig. 96, A). While the cells of the endosperm go on dividing, these few grow enormously for some time without dividing. After a time, however, each one divides into two, of which the upper one (at the micropyle end of the sac) is very small. Very soon this latter cell divides again, first by a transverse wall and then by two vertical ones at right angles to each other. There is thus formed the **neck** of the archegonium (Fig. 96, N), which consists of eight cells, arranged in

four tiers, two cells deep. The lower cell is called the **venter**, and for some time after the upper small cell is cut off it continues to grow. Just previous to fertilization, about the end of June of the second year, it cuts off a very small cell, just beneath the neck, which is called the **ventral-canal cell** (VC). The lower and much larger cell of the venter is the **ovum, oosphere,** or **egg-cell.**

The ovule is now ripe and ready for fertilization, and at this stage it has the following structure: externally it is limited by a single integument (Fig. 96, I), enclosing a thin layer of nucellus (N), which

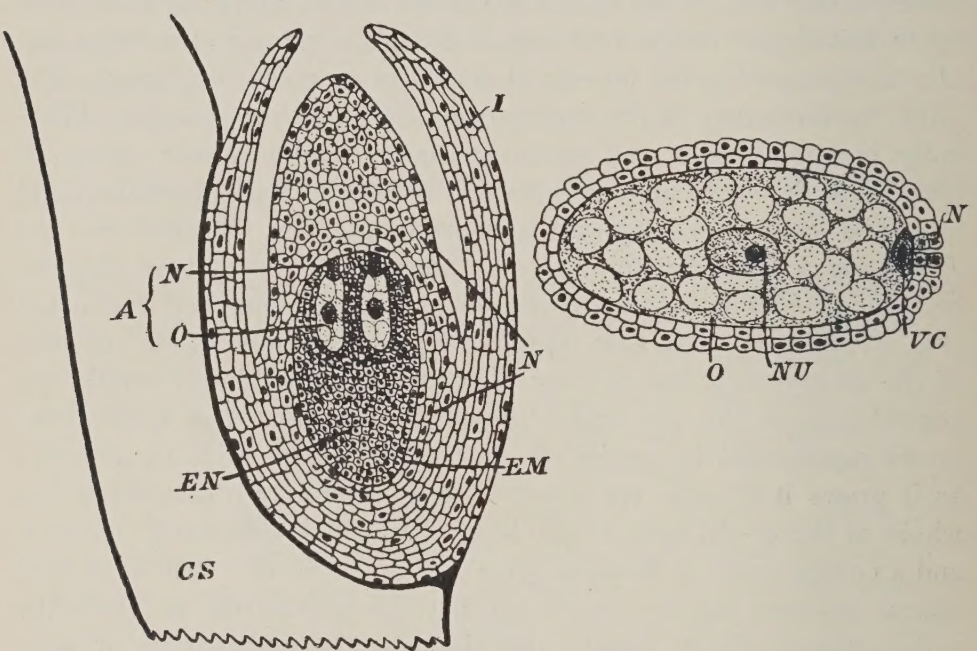


FIG. 96. The left hand figure represents a median longitudinal section through a two-year-old ovule of *Pinus sylvestris*. Magnified 300 times. A=archegonium; CS=ovuliferous scale; EM=embryo-sac; EN=endosperm; I=integument; N (right hand)=nucellus; N (left hand)=neck of archegonium; NU=nucleus; O=ovum; VC=ventral-canal cell of the archegonium, underneath the neck N.

is prolonged up into a conical mass towards the micropyle. Within the nucellus is the embryo-sac (EM) filled with endosperm (EN), and at the micropylar end of this four or five archegonia (A). These latter are the essential portion of the female organs of reproduction, for it is their ova (O) which become fertilized by the generative nuclei of the pollen grains, and from which the embryo arises after fertilization.

The embryo-sac of *Pinus* thus differs from that of an angiosperm in the development of the endosperm before fertilization has taken place,

and in the presence of four or five archegonia, instead of one, or of what represents the vestiges of one (supra, p. 134).

The formation of the archegonia is completed by about the middle of June of the second year, just previous to fertilization. The act of pollination and fertilization will be better understood after we have considered the structure of the male cone.

(*b.*) The Male Cone.

Like the female cone, each male cone consists of a central axis (Fig. 97, A) bearing a few scale leaves (SL) at its base, and the reproductive leaves or sporophylls arranged spirally along the greater length of the axis. We have seen already that each cone is to be regarded as a modified branch of limited growth, while the female cone is a modified branch of unlimited growth. The male cones are borne in a cluster at the base of a lateral vegetative axis (Fig. 97, I, C), while the upper part of the axis bears the vegetative leaves (F); the relation of the cones to the axis is the same as that of the branches of limited growth which bear the vegetative leaves, and both arise in the axis of a scale leaf (SL). But whereas the unmodified branches in the upper part of the axis bear ordinary vegetative leaves, the elongated branches of the lower part bear the modified staminal leaves or sporophylls (S), upon the under surface of which the pollen-sacs (P) or microsporangia are developed.

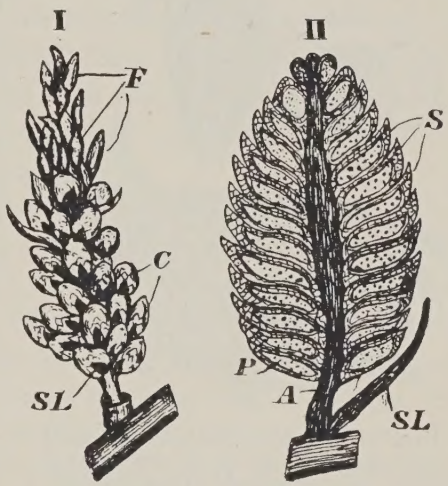


FIG. 97. I. Cluster of male cones of *Pinus sylvestris* (Scotch Fir). C=cones; F=foliage leaves; SL=scale-leaf. II. A median vertical section of a single male cone. A=axis; P=pollen-sac; S=staminal leaves; SL=scale leaf.

Each staminal leaf (sporophyll or stamen) is borne on a small and short filament, and on its under surface are two swellings, the pollen-sacs (Fig. 98, P). As seen in vertical section (Fig. 98, I) each sporophyll is decidedly leaf-like in structure, and the pollen-sac wall (P) is composed of a single layer of parenchymatous cells. The cavity of the pollen-sac is filled with the pollen grains (M). These latter are liberated in May or early June by the dehiscence of the

pollen-sacs, which split open along the middle line and in the plane of their greatest length.

We must now consider the development of the pollen-sacs, because it is only the possession of such knowledge that enables us rightly to understand their homologies or morphological identity with the pollen-sacs of angiosperms or the microsporangia of cryptogams. Each pollen-sac arises from a small group of cells which forms an eminence on the under surface of the sporophyll, and since there are two pollen-sacs there will be of course two of these little eminences or groups of cells on the sporophyll. One cell of each of these groups, immediately beneath the epidermis, rapidly becomes bigger than the rest and then divides up a great many times, giving rise to a mass of cells with prominent nuclei known as the **pollen mother-cells.** The innermost layer of the tissue of the group surrounding the archesporium, or later the pollen mother-cells, is rich in proteids and forms a **tapetum,** which becomes disorganized and its nutritive substances absorbed by the growing pollen mother-cells. At first the wall of the pollen-sac is several layers thick, but before it reaches maturity all except the innermost one is absorbed, being used as nutritive matter for the pollen-mother cells. The changes just enumerated begin in very early spring, and about May the pollen mother-cells divide up and form four pollen grains in each, in the same way as in angiosperms.

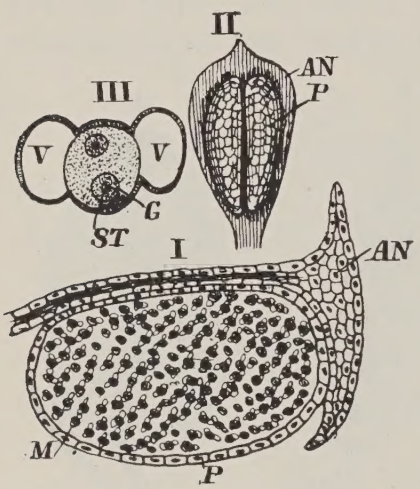


FIG. 98. I. A median longitudinal section of a pollen-sac of the male cone of *Pinus*. AN = staminal leaf (sporophyll); M = pollen grains (microspores); P = wall of pollen-sac. II. Under surface view of the staminal leaf of *Pinus*. AN = staminal leaf; P = pollen-sac. III. A pollen grain in optical section. G = generative nucleus; ST = stalk-cell; V = air vesicle. The upper nucleus is the vegetative one.

The pollen is formed in immense quantities, and in pine districts in May or June may be seen floating in great clouds through the atmosphere. Pines are wind-pollinated, and in order to ensure the chances of pollination being increased, the pollen is formed in far greater quantities than is actually necessary for the act itself, since, in such a mode of pollination, the greater portion of the pollen must be wasted and never reach the ovules at all.

The pollen grains (Fig. 98, III) are peculiarly modified in adaptation to their wind-borne mode of pollination. If we examine some pollen under the microscope we find that each grain has two large lateral vesicles (v) developed upon it, each of which is as large or larger than the pollen grain itself. When the grain is ripe these vesicles are filled with air, so that the specific gravity of the grain is very much reduced thereby. In other words, the surface of the grain is much increased without any corresponding increase of its weight, so that it floats more readily in the air than it otherwise would do. The wall of the pollen grain consists of two layers, an inner cellulose one and an outer cuticular one. In the course of development the outer wall becomes separated from the inner one at two places by the secretion of a fluid; as this increases in quantity the separation between the two layers becomes greater, so that two little blisters are formed. The liquid is next absorbed and the spaces become filled with air by the time that the pollen grain is ripe.

When the pollen grain is first formed after the division of the pollen mother-cell, it is a single cell with one nucleus, but before it is ripe important changes take place within it, by which it becomes converted into a five-celled structure. First a very small cell is cut off at one end of the grain, and this is followed by the cutting off from the large cell of the grain of two other small cells immediately above the first one. There is thus produced a row of three cells, of which the last formed or terminal cell of the row grows bigger, while the other two (the two first formed) collapse and ultimately disappear, without playing any part in the economy of the grain. The two cells which collapse are called the **prothallial cells**, because the only intelligible interpretation of their very transitory presence, in the light of comparative development, is that they represent the vestigial remains of the male prothallium of cryptogams. The third cell of the row then divides into two, forming a small **stalk-cell** (Fig. 98, III, ST) and a larger **terminal cell** (G), which grows until it reaches halfway across the grain. The stalk-cell plays no obvious part in the economy of the grain and later disappears; and for the same reasons that we interpret the prothallial cells as representing a reduced prothallium, we also interpret the stalk-cell as representing a reduced male organ or antheridium.

The pollen grain is now ripe, and we see that it is much more complex than the pollen grain of an angiosperm, for it contains no less than five cells, i.e. the two prothallial cells, the terminal and stalk-cells, and the large vegetative cell forming the main part of the grain itself.

(F.) Pollination and Fertilization.

The dehiscence of the pollen-sacs takes place about the end of May or the beginning of June, and at the same time the axis of the first-year female cones (young ones) undergoes elongation, so that the ovuliferous scales are carried slightly apart ; thus a channel is formed for the passage of the pollen, which is blown about in all directions by the wind, down to the micropyle of the ovule. At the same time that the axis of the cone elongates, the lips of the micropyle of the ovules open widely, so that a relatively broad passage is left leading to the nucellus of the ovule ; the nucellus secretes a liquid from its apical surface, which serves partly to entangle and partly to nourish the pollen grains. After the pollen has been blown down to the ovules between the ovuliferous scales, some of it adheres to the lips of the micropyle ; a little later and the lips bend inwards, closing the orifice of the micropyle, and carrying the pollen grains into contact with the nucellus. The pollen is thus enclosed in a small chamber and bathed in the nutritive liquid secreted by the nucellus, and under these conditions the germination of the grains begins. The first change in germination is the formation of a pollen-tube by the protrusion of the inner cellulose wall, just as in angiosperms. The tube very slowly grows through the nucellus and reaches the archegonia. In *Pinus* the growth of the tube is very slow, and although it is a very short one, it does not reach the archegonia until the June of the following year, viz. thirteen months after pollination. This is not the case, however, in all gymnosperms, for in the spruce fir and others the interval between pollination and fertilization is about six weeks. Soon after the pollen-tube is formed the vegetative nucleus of the pollen grain passes into it, but becomes disorganized and plays no further part. The large terminal cell in the grain then divides into two, each daughter-cell of which is called a generative cell, and the nucleus of which becomes large and granular. The stalk-cell then disappears, and the generative cells are set free and float down into the pollen-tube, at the free extremity of which they remain until the tube reaches an archegonium.

By the time the pollen-tube reaches the embryo-sac the latter is fully ripened and has the structure already described (supra, p. 156). The pollen-tube then pierces the wall of the embryo-sac just above the wall of an archegonium ; it then continues to grow, and passes between the cells of the neck, absorbs the ventral-canal cell, and reaches the

large vacuolated ovum. One of the two generative nuclei then passes out, and, travelling through the protoplasm of the ovum, ultimately reaches its nucleus, with which it fuses. Fertilization is now effected, and the ovum, now called **oospore**, develops into a pine-seed.

(G.) Development of the Embryo.

In *Pinus* the ovum does not surround itself with a cell-wall after fertilization, but the nucleus passes to the bottom of the ovum (Fig. 99, I, O), and there divides twice, the plane of the second division being at right angles to the first. There are thus formed four nuclei lying in the same plane, so that in a vertical section only two can be seen. Three successive divisions, at right angles to the long axis of the embryo, next take place, so that four columns of four tiers of cells, one above the other (1, 2, 3, 4), are formed. Of these, the three lower tiers of cells become surrounded by cell-walls, while the four cells of the upper one remain naked (Fig. 99, II). The great mass of the ovum does not divide, and takes no part in the formation of the embryo other than to serve as a source of limited nourishment for the developing embryo.

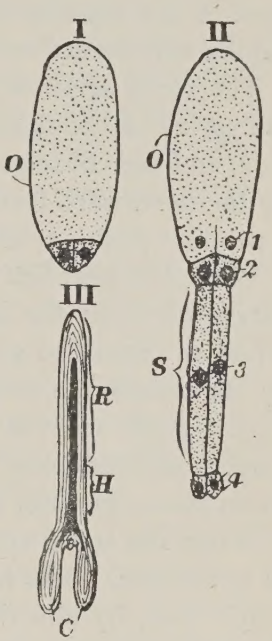


Fig. 99. The developing embryo of *Pinus sylvestris*. C=cotyledons; H=hypocotyl; O=ovum; R=root; S=suspensors.

The four free nuclei (1) at the top tier become disorganized, and the cells of the second tier (2) undergo no change. The cells of the third tier (3) become very much elongated, and form the **suspensors** (S); the formation of the suspensors thus pushes the lowest tier of cells (4) deep into the endosperm. The lowest tier of cells (4) divides up a few times, and it is from this group of cells that the embryo arises. In *Pinus* the four suspensors separate slightly from one another, and the four groups of cells, one at the end of each suspensor, for a time develop as four separate embryos. And since there are four or five archegonia in each embryo-sac, each of which may be fertilized, it follows that there may be from sixteen to twenty embryos developing side by side in the same embryo-sac. But only one of these becomes

a fully formed embryo, for the others lag behind in the race, and ultimately become crowded out and absorbed by the most robust among them. The victorious embryo continues to divide and grow, and by September of the second year it has attained the form figured in Fig. 99, III. It has a very elongated radicle (R) traversed by an axial vascular stele, its apex directed towards the micropyle of the ovule. The radicle below is continuous with the hypocotyl (H), which bears a number of short cotyledons (C), twelve to sixteen in all, of which, of course, only two can be seen in section. The plumule or apex of the stem is very small at this stage, and is seen as a minute papilla surrounded by the bases of the cotyledons.

The seeds are now ripe, and in this condition they will remain until the spring of the third year, when by the elongation of the axis of the cone and the consequent separation of the ovuliferous scales, preceded by the downward turning of the cone as a whole, so that it assumes a pendant position, they are liberated and fall to the earth.

While the seed has been ripening internally, externally the wing-like outgrowth from the integument of the ovule develops still more and forms an expanded wing which offers a great surface to the wind, and by its means the seeds are often carried a great distance from the parent plant, in even a gentle breeze. In this way the seeds are dispersed, and the keenness of the competition for a living, which ensues when plants grow in a crowded manner, is much lessened.

When the seeds are liberated and fall into a suitable soil, they begin to germinate. The radicle grows out through the micropyle, and the cotyledons, by absorbing the remaining endosperm, grow and burst open the testa or seed-case, and direct themselves upwards; at first the testa is carried up with them, but it is soon thrown off, and the cotyledons are then exposed to light. The plant can now obtain its own food-material, and very soon the apex of the stem begins to grow upwards.

CHAPTER X

CRYPTOGAMS.

(A.) PTERIDOPHYTA.

LITERALLY translated, the word cryptogam means 'hidden marriage,' and was applied by Linnæus to all those plants, such as ferns, mosses, club-mosses, and algæ, which do not possess flowers, and in which the processes and more immediate results of fertilization were obscure or unknown. The term in its original significance is no longer correct, for with the introduction of the microscope the processes of fertilization gradually became known in phanerogams and cryptogams alike. The term, however, like many others in scientific nomenclature, is retained in spite of its inapplicability, because it is more convenient so to do than to substitute for it a new and more correct one.

The cryptogams include a large number of plants of diverse characters and habits; some of them are microscopic in size and of the simplest structure, others are very tall and of a complexity of structure attaining to that of the phanerogams. The more complexly organized among them possess vascular strands, and these are grouped together as the **Vascular Cryptogams**, while the others in which no vascular bundles are developed are grouped as the **Cellular Cryptogams.**

Placed at the top of the cryptogams is the class Lycopodiaceæ, containing *Lycopodium* (club-moss), *Isoetes*, and *Selaginella*. All these genera are the living representatives of groups of plants of immense antiquity, that flourished in the Carboniferous Period of sixty million years ago, more or less. In this period of geological time these plants were much more numerous in genera and species than they are to-day, and those that we know are but the last traces of a once prodigious group now verging to extinction. In the Coal Measure Epoch of this period certain plants possessed upon the upper surfaces, and near the axils of their leaves, little leaf-like outgrowths, called ligules. Among living cryptogamic plants, *Selaginella* and *Isoetes* are the only two which have retained these ancient structures, and in the former plant they are only clearly seen upon the young leaves as they quickly wither and disappear from the older ones, thus foreshadowing their ultimate disappearance in some more or less remote future generation.

Hence the study of *Selaginella* is of more than usual interest, for it

is one of the few living connexions that link together the present and the past; and in working through its anatomy we shall endeavour to discern to what extent it has retained the characters of its remote ancestry, and in what manner it foreshadows an approach to those of a later advent and more complex organization.

SELAGINELLA.

1. External Characters.

(A.) Shoot and Root.

The habit of the different species of *Selaginella* varies somewhat; some are minute and creeping, but a few tropical ones climb up the trunks of trees, and are thus ascending, and may reach a height of seventy feet. The majority are tropical, and inhabit the damp undergrowth of the forests, while only a comparatively few inhabit Europe. One species, *S. spinosa*, inhabits the boggy districts of the moorlands of our own country. Many of the tropical species are cultivated in hothouses.

Selaginella (Fig. 100) possesses a creeping stem (S), which creeps along just above the surface of the ground; it is much branched, but in a single plane, so that the plant has a dorsal (upper) and a ventral (lower) aspect, and hence the term **dorso-ventral habit**. The branching is apparently a dichotomy, i. e. the main axis appears to divide into two equally formed branches, but as a matter of fact it is a monopody, i. e. the main axis grows more vigorously than the branches which arise laterally from the stem. The apparent dichotomy is due to the fact that the lateral branch, which arises immediately behind the apex, at first develops at a rate approximating to that of the main axis above its origin, and thus the main axis and lateral branch are at first equally developed.

The stem and branches bear a large number of leaves (L and L′), closely packed at the growing points, but more widely separated on the older portions. The leaves are of two forms, and are arranged in two horizontal planes: a ventral (lower) row of larger leaves (L) on either side of the stem, and a dorsal (upper) row of smaller leaves (L′) alternating with the larger. The larger and smaller leaves of one side alternate with the corresponding form of leaf of the other side, so that a pair of leaves consists of one large and one small one. Each leaf is

traversed by a single central nerve or midrib, and on the upper surfaces of the younger leaves, apparently arising from the axil of the leaf, but in reality from the leaf itself, is a small scale-like **ligule**; on the older leaves these wither up, and often quite disappear.

From the side of the stem, at points where the branches arise, there are given off root-like structures (R) which grow vertically downwards. These are the **rhizophores**; they are destitute of leaves, and differ from roots in the absence of a root-cap. Upon coming into contact with the soil, they give origin to **roots** (RT) with root-caps, which

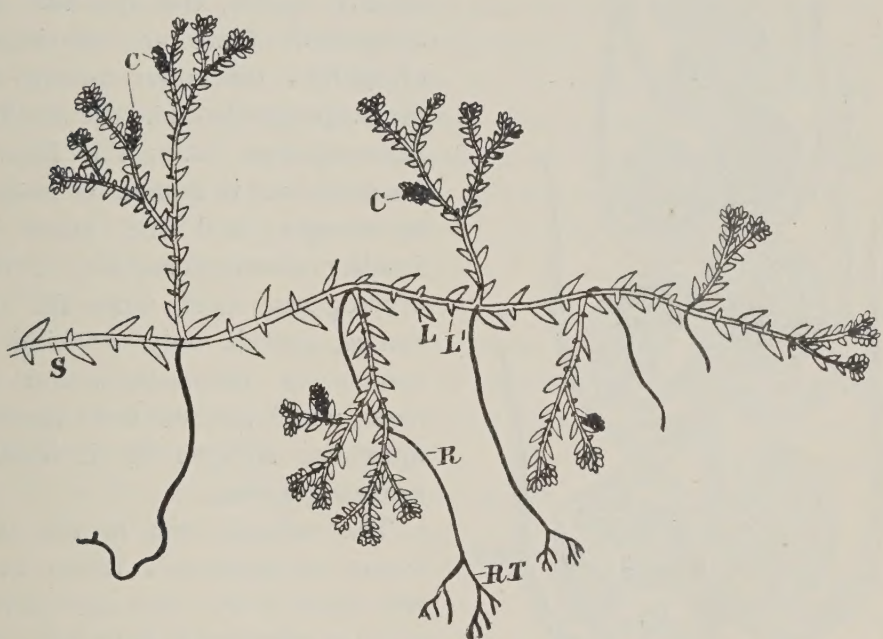


FIG. 100. A plant of *Selaginella*. C=cones; L=larger leaves; L'=smaller leaves; R=rhizophore; RT=root; S=stem.

penetrate the ground and function as the absorbent organs of the plant.

Some of the branches, instead of creeping along the surface of the ground, rise vertically, and have the leaves near the apex symmetrically arranged. These are the **cones** (C) or reproductive branches, and their vegetative nature is very apparent; it is easy to see that if these are the reproductive cones, they are but modified vegetative branches.

(B.) REPRODUCTIVE ORGANS.

The reproductive branches (Fig. 101) differ from the vegetative ones in that the leaves are all of one form, and that in the axils of the upper

leaves (**sporophylls**) certain globular bodies (**sporangia**) (MI and MA) are borne. The sporangia (spore-cases) are borne either in the axil of the leaf or upon its upper surface very near the axil, but in the majority of cases they arise from the stem, and later become shifted to their final position; in a few instances they arise directly in the axil of the leaf. The sporangia are globular cases containing a larger or smaller number of reproductive bodies, the **spores**. In *Selaginella* there are two kinds of spores: the larger **macro-** or **megaspores** (MG) and the smaller **microspores** (MS); the former are contained in **macro-** or **megasporangia**, and the latter in smaller **microsporangia**. Some cryptogams, most ferns for instance, contain only one kind of spore; in contradistinction to these, which are said to be **homosporous**, *Selaginella* is called **heterosporous**.

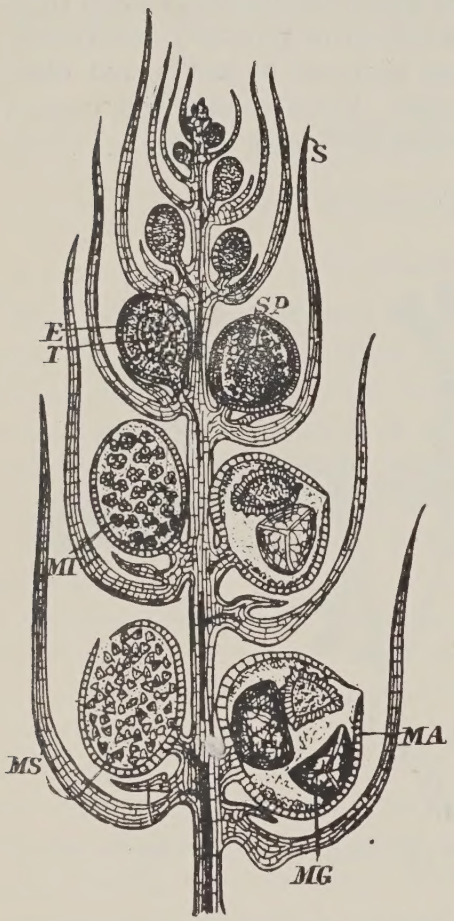


FIG. 101. Median longitudinal section through the cone of *Selaginella*. Magnified 300 times. E=outer wall of sporangium; MA=megasporangium (macrosporangium); MG=macrospore; MI=microspores; MS=microsporangium; S=sporophyll; SP=macrospore mother-cell; T=tapetum.

The arrangement of the two forms of sporangia varies with the species: in a few species the microsporangia are found on one cone, and the macrosporangia on another; in *S. Kraussiana* the macrosporangia are situated on the lower sporophylls of the cone, and the microsporangia on the upper; in *S. helvetica* the macrosporangia are arranged along one side, and the microsporangia on the other. The macrosporangia are rounded and somewhat tetrahedral in form, greenish or light brown in colour, and contain four macrospores. The microsporangia are rounded, orange in colour, and contain a large number of microspores comparable in size to pollen grains. At a certain stage in the maturation of the spores, the

sporangia split open (dehisce) in a plane which is parallel with that of the sporophylls, and the spores are liberated—the microspores at an earlier stage than the macrospores.

2. Internal Structure.

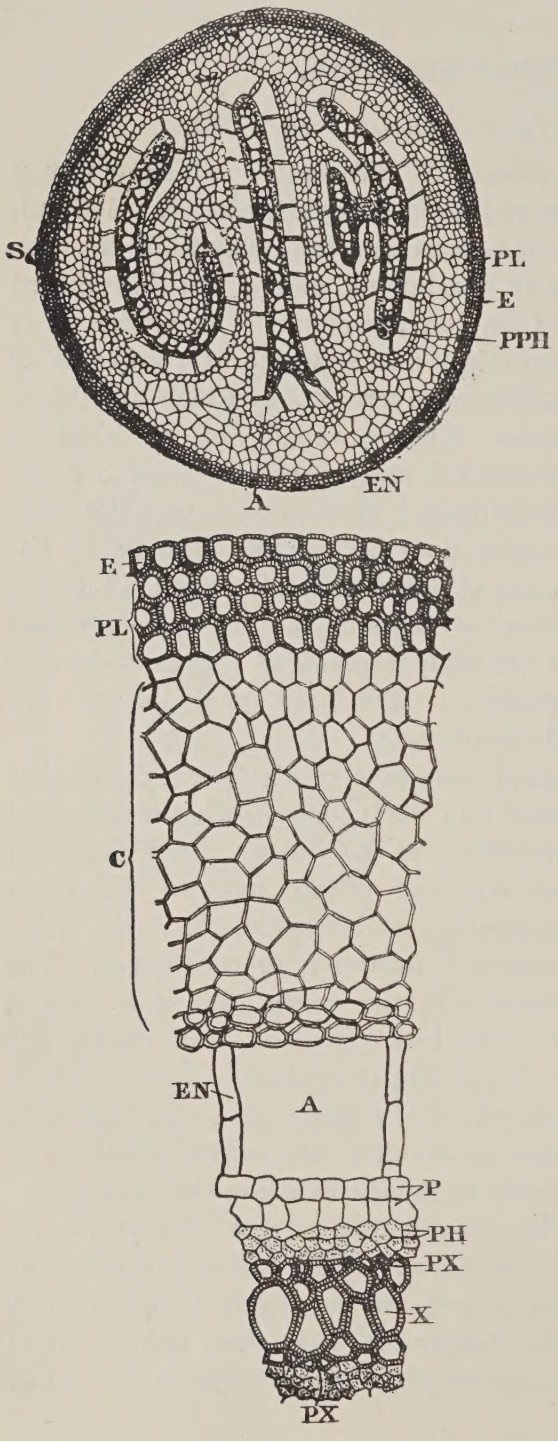
(A.) Minute Structure of the Stem.

A transverse section of the stem of *S. Wildonovii* will show that it is limited externally by a not well-defined epidermis (Fig. 102, E), the cells of which are prosenchymatous, and the outer walls of which are cuticularized; the cuticle is continuous, and is not interrupted by stomata, since these are absent on the stem. The epidermis is immediately followed by the cortical tissue, which is composed of prosenchymatous cells, the peripheral layers (PL) of which are thick-walled and lignified, but become thinner walled and of cellulose, centrally (C). Occupying the central portion of the stem are the steles (S), three in number and elliptical in outline, so that the stem is **polystelic**. The cortical tissue does not extend right up to the steles, but leaves a uniform space (A) round each one, which is bridged in several places by trabeculæ of parenchymatous tissue, called **lacunar tissue** (EN). This probably represents the **endodermis** (**bundle sheath**) of other cryptogams. The large spaces left between the trabeculæ are probably filled with gases.

Examination of longitudinal preparations of the stem shows that the vascular strands are cauline and not common, i.e. are confined to the stem, and do not bend outwards to the leaves. Each stele can be followed continuously from one end of the stem to the other, whereas in the majority of phanerogams the vascular strands, when traced upwards, sooner or later lead outwards to the leaves. The bundles are, however, connected with the leaves, but it is only a small branch of the stele which is thus connected, and which runs through the leaf as a single small vein or midrib. At the points where the lateral branches arise from the stem the steles fuse with each other; at these points they send out to the lateral branches of the stem an equal number of steles to those traversing the main axis.

The structure of the stele is very different to that of anything we have studied among the phanerogams. The various constituents (Fig. 102) of which it is composed are arranged concentrically, i.e. the pericycle (P) as the outermost ring, the phloem (PH) as one within this and surrounding the central xylem (X). The

arrangement of its parts is, therefore, different to that in the root, where the phloem and xylem are situated on alternate radii, or that in the phanerogamous stem, where the phloem, cambium, and xylem lie on the same radius, one externally to the other.



The pericycle (Fig. 102, P) is composed of an irregular band of slightly elongated or squarish parenchymatous cells, with thin cell-walls, and protoplasm with contained chlorophyll grains; it abuts immediately on the trabeculæ of the endodermis (EN), and lies externally to the phloem (PH). This latter is composed of elongated cells, with thin cellulose walls, scanty protoplasm, but no sieve-plates. Centrally lies the primary xylem (X), composed exclusively of tracheides, with thick, lignified walls, and elongated, slit-like pits arranged in a scalariform manner. Cambium is not formed, and

FIG. 102. Transverse section of stem of *Selaginella Wildonovii*. The upper figure represents a complete section, magnified 80 times, and the lower one a portion of the section only, magnified 300 times. A = air-space; C = cortex; E = epidermis; EN = endodermis; P = pericycle; PH = phloem; PL = lignified peripheral portion of cortex; PPH = pericycle and phloem; PX = protoxylem; S = steles; X = xylem.

so secondary xylem is never developed. There is no pith. The protoxylem strands (PX) are several in number, and instead of being situated *centrally* to the primary xylem as in phanerogams, they lie at the *periphery* of it. Examination of a series of sections, commencing from a little way behind the apex and passing backwards to the mature stem, shows that the protoxylem strands are the first lignified portions of the primary xylem, and that, as the stem increases in age, the xylem progressively lignifies from the protoxylem inwards, i.e. develops **centripetally.** This mode of development of the xylem is characteristic of that of the phanerogamous root, and is unlike that of the phanerogamous stem, in which the development is characteristically centrifugal, i.e. from the centre outwards. This type of stele, characterized by the absence of pith, the centripetal development of the xylem, and the want of differentiation of the vascular bundles, is an ancient one, for it characterizes that of the stems of some carboniferous plants; and it constitutes a clear boundary between the vegetative structure of the flowering and flowerless plants.

Steles which contain several protoxylem strands are said to be **polyarch.**

(B.) Minute Structure of Rhizophore and Root.

The peripheral tissues of the rhizophore and root are similar to those of the stem; there is the same trabecular endodermis, and the pericycle is alike in either case. In details of structure the rhizophore and root are almost the same, and the former differs from the latter only in the absence of a root-cap. Both organs differ from the stem in that the stele is **monarch,** i.e. contains only one protoxylem group. The rootlets of many of the plants of the carboniferous period possessed such steles, so that it is a very ancient structure. The protoxylem strand is situated laterally, and the later-formed xylem forms a central mass, almost entirely surrounded by the phloem, which is interrupted opposite the protoxylem.

Median longitudinal sections through the apex of a root show the presence of a root-cap. This is absent at the apex of the rhizophore.

(C.) Minute structure of the Leaf.

The structure of the leaf is comparatively simple: it is limited on the upper and lower surfaces by an epidermis composed of somewhat radially elongated cells on the former surface and of smaller cells on

the latter; chlorophyll grains are present in all the epidermal cells, as in the stem, and are of markedly large size. Stomata are absent from the upper surface, and those on the lower are concentrated along the midrib, and the limiting guard-cells are small. The mesophyll consists of a nearly uniform parenchyma with intercellular spaces; and traversing it is the single vein or midrib, composed of a central strand of tracheides, surrounded by phloem, and the whole enclosed by a bundle sheath.

(D.) Apical Development.

(*a.*) The Stem.

In *Selaginella* the apical development of the stem is quite different to anything we have so far studied, and, moreover, it varies among different species of this genus, in some approaching in a remote manner that of the phanerogams, but in the majority it is typically cryptogamic.

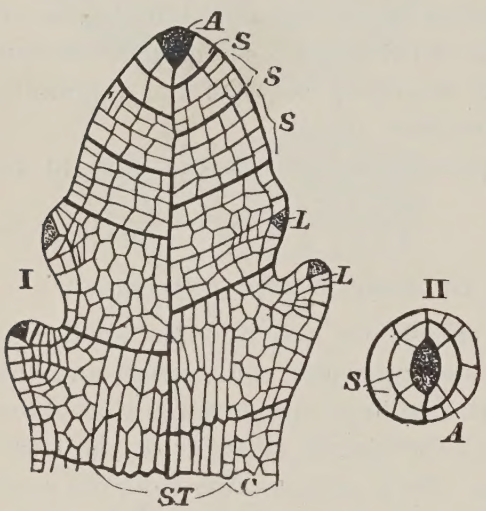


Fig. 103. Apical development in stem of *Selaginella*. I. Median longitudinal section through apex of stem. II. Transverse section across apical cell. Magnified 300 times. A= apical cell; C=cortex (extra-stelar tissue); L= developing leaves; S=segments derived by division of apical cell; ST=stele.

Instead of an apical meristem composed of a group of cells, there is in most species only a single cell, the **apical cell** (Fig. 103, A), situated at the extreme summit of the apical cone. The form of this cell varies according to the particular habit of the plant, and in those with the usual four-row arrangement of the leaves, and a distinctly dorso-ventral habit, the cell is lens-shaped, i.e. two-sided, in transverse section (Fig. 103, II), while in those, as in some individuals of *Selaginella Martensii*, in which the habit tends to become shrubby, and the dorso-ventral one more or less indistinct, it is a three-sided pyramid, with its apex directed backwards.

We will first consider the two-sided, lens-shaped cell. As seen in transverse section it is biconvex in form (Fig. 103, II); when viewed in median, longitudinal section (Fig. 103, I) it is conical, with its base

directed forwards. The apical cell cuts off segments (S) alternately right and left ; then both apical cell and segments grow ; by continual segmentation and concurrent growth of the apical cell there are formed behind it two rows of segments, meeting by their inner surfaces along the middle line ; this mass of segments forms an **apical cone**, at the summit of which is the apical cell, and at the base the youngest leaves (L) or branches in the earlier stages of their development. But each of these segments not only grows but also divides repeatedly, by anticlinal and periclinal walls, so that they become masses of cells in a very little time ; the limits of each segment can, however, be detected by the greater thickness of the walls, and in the earlier ones by the arrangement of its constituent cells. In some of the lower segments the tissue becomes differentiated into a central (ST) and a peripheral portion (C), mainly distinguished by the form of the cells, which is the result of a greater or lesser activity of the segments in dividing. The central portion if followed downwards becomes further differentiated and gives rise to the steles, while the peripheral portion forms the epidermis, the cortex, and lacunar tissue.

If the apical cell is a three-sided one the main features of segmentation are the same, but instead of two segments being cut off there are three, one from each side of the pyramid.

The leaves arise by the outgrowth and division of a group of cells at the periphery and at the base of the apical cone. The branches arise in a similar manner, but in front of the youngest leaf and *behind the apex*; their origin from behind, and not at the apex, shows that the system of branching is monopodial (supra, p. 6). In a true dichotomy the apex (apical cell) divides into two equal parts.

In *Selaginella spinulosa* there is not an apical cell, but a row of cells passing round the apex: inasmuch as such a row approximates to a group of cells, it remotely approaches the condition of the apical meristem of phanerogams.

(*b.*) The Root.

The apical development of the root is by means of a three-sided pyramidal cell, with its base directed outwards. The vascular strands and cortical tissues arise from it, in the same manner as those in the stem, but the apical cell also cuts off segments from its base which by growth and repeated divisions give rise to the root-cap : this latter is continually worn away in front by attrition with the soil, and is replaced by new segments behind.

The roots arise from the extremity of the rhizophores as soon as these reach the ground, by endogenous origin from the pericycle of the stele. In some species (*S. Martensii*) the rhizophore bears a swollen extremity from which the roots arise.

The lateral rootlets arise quite close to the apex of the main roots, and are in fact covered by the hinder margin of the root-cap; they arise from superficial tissues, and are, therefore, exogenous in origin. But this is exceptional, and does not hold true of vascular cryptogams as a whole.

3. Organs of Reproduction.

(A.) Mature Structure of Sporangia and Germination of the Spores.

The sporangia (Fig. 101) are hollow box-like organs, the position and general form of which have already been indicated. Their wall is composed of three layers, of which the outer one (E) is the strongest, and is composed of cells radially elongated and with thick walls; the layer next within this consists of very flat cells; and the innermost layer (T) is made up of radially elongated cells with dense protoplasmic contents, and is called the **tapetum**. The tapetum is a nutritive tissue from the products of the disorganization of which the contained spores are nourished; in most cryptogams this layer is absorbed before the spores are ripe, but in some species of *Selaginella* it is persistent until the spores are matured. The structure of the microsporangia and the macrosporangia is the same, except that they differ in size.

If we examine the contents of a macrosporangium (megasporangium) (Fig. 101, MA) a little before it is quite ripe and before dehiscence, we shall find that it contains four tetrahedral bodies (MG), arranged in a group like four cannon balls, i. e. three in one plane and the remaining one in a higher plane, in the axis round which the lower three are arranged. Each of these is a **macrospore** (**megaspore**), and their external surface is marked by wart-like excrescences. At a period just antecedent to completed maturation each spore is a single cell, consisting of a central mass of protoplasm with a nucleus and enclosed by two cell-walls, of which the inner one or **endospore** is thin and of cellulose, and the outer or **exospore** is thick, cuticularized, and yellow in colour.

An examination of a microsporangium (MI) at the same stage will reveal the presence not of four, but of very numerous, minute spores

(MS), arranged in groups of four (see Fig. 101, second sporangium from bottom of cone), but later more or less indiscriminately scattered (see sporangium below). Each spore is a single cell, with two walls, and is essentially the same in structure as a macrospore, but very much smaller.

The dehiscence of the sporangia occurs, in either case, at different stages in the maturation of the spores. The microsporangium dehisces by a split parallel to the plane of the sporophyll, at the stage when the microspore is still a single cell. The microspores thus liberated undergo further changes, collectively spoken of as **germination**, if they fall upon moist soil. The macrospores, on the other hand, do not leave the macrosporangium until their germination has proceeded to a considerable extent; though apparently a detail, this fact is important, because, as we shall see when we have finished our study of cryptogamic reproduction and life-histories, it foreshadows the phanerogamic condition.

We shall study first the germination of the macrospore, because in its fully formed condition it is less modified than the microspore. The first change that indicates its commencing germination is the division of its nucleus into two; which again divide, and again repeatedly, until there are many nuclei lying free in the protoplasm in the apical half (towards the angle of the tetrahedron which is in contact with the sister spores) of the spore. Then cell-walls begin to appear between the nuclei, and thus form a parenchymatous tissue (Fig. 104, P), which at this stage forms a mass in the upper half of the spore; in some species the macrospores are liberated from the macrosporangium at this stage, but in others the process of nuclear division and cell formation proceeds until all the spore is filled before dehiscence of the sporangium takes place. The tissue thus formed is called a **prothallium**, and the student will do well to recall the fact that the endosperm within the embryo-sac of *Pinus* is developed in the same way, i. e. by the repeated divisions of the nucleus of a single cell and the formation of cell-walls only when that process has nearly finished. And just as in the endosperm of *Pinus*, so in the prothallus of *Selaginella*, certain of the prothallial cells at the apex of the spore, at first only one, but subsequently two or three others, become much larger than the rest. Then one of these larger cells (Fig. 104, 1, A) divides into two by a transverse wall (parallel to the surface of the spore), of which the upper cell divides again by two longitudinal walls at right angles to each other, and each of these four cells again divides

by a transverse wall into two. Thus, at this stage (Fig. 104, II), we have a large lower cell (O), with eight smaller cells (N) above, arranged in two tiers round a central axis ; the eight cells thus constitute a **neck.** The lower cell then sends an upgrowth (NC) in between the eight cells, and thus occupies the lumen of the neck ; this upgrowth becomes segmented off from the larger cell, and is called the **neck-canal cell** (NC). The larger cell cuts off another small cell by a transverse wall, which lies immediately behind the neck-canal cell ; it is called the **ventral-canal cell.** The remaining lower cell is the **ovum.** The

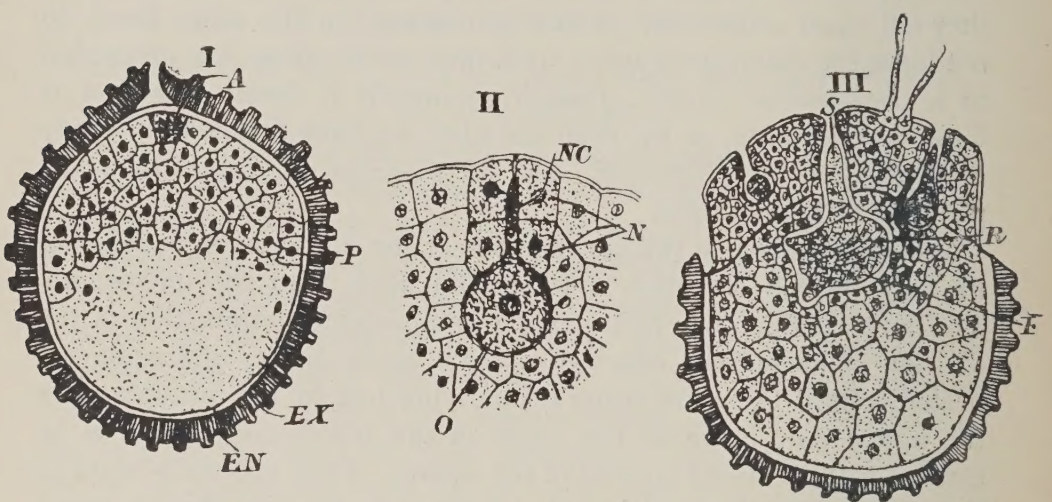


FIG. 104. Germination of the macrospore of *Selaginella*, and development of the embryo. I. The formation of the prothallus and development of archegonium. II. Later stage in the development of an archegonium. III. A mature gametophyte with embryos in different stages of development. The embryo to the left is at the segmentation stage, and that to the right has formed the suspensor. The one in the middle has formed the rudiments of all the organs of the sporophyte. The two cotyledons can be seen projecting outwards on its left, with the apex of the stem between them, and the apex of the root on its extreme right. The suspensor passes vertically upwards. A=developing archegonium ; EN=endospore ; EX=exospore ; F=foot ; N=neck of archegonium ; NC=developing neck-canal cell ; O=ovum ; P=developing prothallium ; R=root ; S=suspensor.

whole group of cells, i. e. neck, ventral and neck-canal cells, and ovum, is called an **archegonium.**

Now a comparison of the development of the archegonium of *Selaginella* from a single prothallial cell with that of *Pinus* from a single endosperm cell, will show that the two structures are almost identical, and that they only differ in the small detail of the neck-canal cell being present in the former and absent in the latter. Hence there can be no doubt that the archegonia of the two plants are homologous[1] organs, and if this is so, then it logically follows that the endosperm of

[1] Morphologically identical.

Pinus is equivalent to the prothallium of *Selaginella*, since both tissues occupy the same relation to the archegonium and arise in the same manner; and it also follows that the embryo-sac of *Pinus* is the homologue of the macrospore of *Selaginella*, since the one is related to the endosperm in precisely the same way that the other is to the prothallium.

A tabulation of the facts may render this clear :—

PINUS.		SELAGINELLA.	
Three or four endosperm cells enlarge at upper part of embryo-sac.		Three or four prothallial cells enlarge at upper part of macrospore.	
The enlarged endosperm cells divide into upper smaller and lower larger cells.		The enlarged prothallial cells divide into upper smaller and lower larger cells.	
Upper smaller cell divides into eight and forms the NECK.	Lower larger cell segments off the VENTRAL-CANAL CELL.	Upper smaller cell divides into eight and forms the NECK.	Lower larger cell by upgrowth and segmentation forms the NECK - CANAL CELL and later segments off the VENTRAL-CANAL CELL.
	The large remaining cell = OVUM.		The large remaining cell = OVUM.

Very often the first archegonium is formed in the incomplete prothallus at the time of dehiscence of the sporangium. But at about the stage when the first or second archegonium is formed, the exospore (EX) ruptures at the apex of the spore, and the prothallium projects slightly but *never completely emerges from the spore.* When exposed to light, chlorophyll is developed, and the prothallium becomes green. The early stages of germination proceed at the expense of certain food-material, in the form of oil drops and starch grains stored up in the protoplasm at the lower portion of the spore; but once chlorophyll is formed the plant can obtain its food from external sources. When the archegonia are formed the maturation of the spore is complete, and its further development depends upon certain structures liberated by the microspores. Hence to them we will next turn our attention.

As has been already stated, the germination of the microspores does not commence before the dehiscence of the sporangium has taken place. As soon as the microspores fall upon damp soil germination commences, the first step in the process of which is the cutting off of a very small cell to one side of the spore, called the **prothallus cell** (Fig. 105, P), for reasons which we shall consider later. The large

cell of the spore then divides by repeated divisions until there are about twelve cells, called the **antheridial cells**, present, and these are arranged in such a way that there are eight peripheral cells (AN), and either four or two central ones (C), according to the species. The central cells then divide repeatedly and form a number of rounded cells, called the **spermatozoid (antherozoid) mother-cells** (S), with large nuclei, and which soon after their formation become invested by a cell-wall. At about this stage the hard outer exospore bursts, and the spore contents are now only retained by the thin endospore. The peripheral cells become disorganized and form a mucilaginous mass in which the spore mother-cells float, and from which they derive nutritive material. The prothallus cell persists throughout. The nuclei of the spermatozoid mother-cells undergo an elongation, by which each becomes converted into a club-shaped body with a limited spiral twist (SP); at the thin end of each nucleus are two protoplasmic threads derived from the protoplasm of the cell. The metamorphosed nucleus is the **spermatozoid (antherozoid)**, and the two threads, which serve as locomotor organs, are its cilia. At about this stage the endospore breaks down, and the spermatozoid mother-cells are liberated upon the damp ground. *Selaginella* inhabits only shady and damp positions, and there is usually a film of moisture upon the soil on to which the mother-cells are liberated; this thin film is sufficient to immerse the cells, so that they in reality float in water. Soon after the liberation of the mother-cells the spermatozoids begin to wriggle about, and the cell-wall becoming dissolved they are liberated into the water, where they move actively about by the lashing of their cilia. Their movement is a double one: in part it is a forward one, in which the narrow end of the spermatozoid is foremost, and in part it is a rotation round its own axis; in fact, it is very similar to that movement of a cricket ball to which juvenile cricketers apply the epithet of 'twister,' because while the ball is moving forwards it is also twisting round. The size of the spermatozoids is exceedingly minute, averaging about the $\frac{1}{2000}$ of an inch long for the body, and

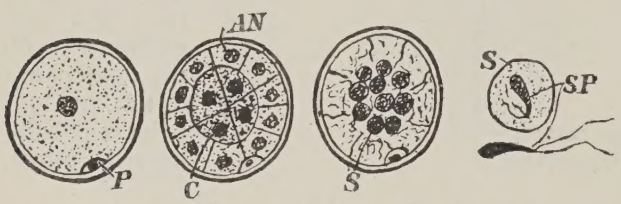


FIG. 105. Germination of the microspore of *Selaginella*. AN=peripheral antheridial cells; C=central antheridial cells; P=prothallial cell; S=spermatozoid mother-cells; SP=spermatozoid.

twice that length for the cilia; the body is, therefore, about half as large again as the human red blood-corpuscle.

The spermatozoids are the ultimate male elements, for it is they which perform the act of fertilization. They thus correspond, alike in ultimate morphological nature and physiological purpose, to the generative nuclei of the phanerogamous pollen-tube. Like the generative nuclei they consist almost entirely of nucleus; the spermatozoid is in fact all nucleus with the exception of the protoplasmic cilia, and the generative nucleus is all nucleus except a very thin film of protoplasm surrounding it. In certain cryptogams (ferns) and in certain animals the cilia and tail respectively of the spermatozoid and the spermatozoon are lost before the actual act of fertilization is completed; hence we may conclude that it is the nucleus alone which is the essential factor in the process, and which is the bearer of hereditary qualities.

Lying in the moist soil immediately beneath, or more or less farther removed from the parent plant, we have then ripe macrospores with their archegonia and ova, and active, motile spermatozoids derived from the microspores. As soon as the archegonia become ripe, the ventral- and neck-canal cells disorganize and form a mucilaginous mass which oozes out from their necks, and the lips slightly open. It is probable that this mucilage in *Selaginella* serves the same purpose as that in the fern, i. e. to attract the spermatozoids in virtue of some substance which it may contain (*chemiotaxis*); but this has not been proved for *Selaginella*, nor has the actual fusion of the spermatozoid with the ovum been observed. There can be no doubt, however, that that which occurs universally throughout the animal and plant kingdom occurs here; i. e. the spermatozoid swims down the canal of the neck, and wriggling its way through the protoplasm of the ovum, fuses with its nucleus.

Comparing now the microspore with the macrospore we find there are certain differences: in the former the only representative of the prothallium of the latter is the single cell cut off on one side from the spore-cell; that this represents a very reduced male prothallium is probable, because its place and manner of formation in the germination of the microspore is similar to that of the first stage in the formation of the female prothallium in the macrospore, which arises by the division of the nucleus in the apical angle of the spore. Moreover, there are some plants (horse-tails) which have male and female prothallia well developed, the former smaller than the latter, but nevertheless very obvious prothallia; and the first stage in the development

of these male prothallia from the spore is almost identical with the cutting off of the single cell in the microspore of *Selaginella.* The single cell thus cut off, therefore, represents not a rudimentary but a vestigial[1] male prothallium. In the prothallium of the macrospore we saw that the ovum, or ultimate female element, is enclosed in a more or less flask-shaped structure, the archegonium, derived with the ovum from the division of a single enlarged cell of the prothallium. Now, in the microspore, the ultimate male elements or spermatozoids are not enclosed in a special organ. But in the male prothallia of the horse-tails and in some ferns the spermatozoids, as we shall later see, are enclosed in a definite and special organ, called the antheridium, which is in every way the corresponding male structure to the female archegonium. And in such plants the antheridium and the spermatozoids arise, just as the archegonium does, from the division of a single prothallial cell. Now it is obvious that the single large cell, borne as it were upon the minute prothallial cell of the microspore of *Selaginella,* and which by repeated divisions gives rise to a group of cells surrounding and including those that give origin to the spermatozoids, occupies in the germination of the spore precisely the same place that the enlarged archegonial cells of the macrospore or the cell just described of the male prothallia do. Hence we must regard this group of cells as the equivalent of an antheridium, and also as the male representative in the microspore of the archegonium of the macrospore; hence their name—**antheridial cells.**

Thus a comparison of the microspore with the macrospore shows that the former is reduced to an almost minimum grade of organization, consistent with the purposes it has to fulfil in the life-history of the plant; and a further comparison of it with the male prothallia of lower cryptogams shows the direction in which this simplification of organization has taken place.

Now a similar comparison of the microspore of *Selaginella* with the pollen grain of *Pinus* will show that in the latter this reduction of the unessential portions has proceeded a stage farther, and that in addition new structures have arisen which are adapted to the wholly terrestrial mode of life that *Pinus* has adopted. We learned that in

[1] There is some ambiguity in the use of these two words. By a rudimentary structure we shall understand one in the course of evolving to a higher and more complex organization, and by a vestigial one a structure in the course of disappearing.

the pollen grain of *Pinus* two little cells, which are called prothallial cells, are cut off from the large cell of the grain, and that these cells persist for a short time and then disappear. Just above them there is cut off another, but larger cell, which itself quickly divides into two, of which that in apposition to the prothallial cell is called the stalk-cell, and the other, which bulges into the protoplasm of the pollen grain, is called the terminal cell. This latter divides and forms two generative nuclei. Now the place in the development of the pollen grain which the two prothallial cells occupy is identical with that of the single one in the microspore of *Selaginella*, and, therefore, represents a vestigial male prothallium; and the stalk, terminal, and vegetative cells are obviously the equivalent of the antheridial cells of *Selaginella*, and represent a reduced antheridium; while the generative nuclei occupy with respect to these in particular, and to the course of development in general, the same relation that the spermatozoids of the microspore do. And hence we must conclude that the pollen grain of *Pinus* is the equivalent, or, in more technical language, is the homologue, of the microspore of *Selaginella.* Thus far, then, the two structures, though differing in certain details, are fundamentally similar. But there are important differences: the spermatozoid reaches the ovum by virtue of its own activity, but the generative nuclei of *Pinus* are carried in a passive manner by a short pollen-tube. Fertilization by means of a motile spermatozoid (**zoidogamy**) is very characteristic of the cryptogams, while that by means of a pollen-tube (**siphonogamy**) is equally characteristic of the phanerogams. Evidently this difference of the mode of fertilization is correlated with the different habits of the two classes. The phanerogams are essentially aëro-terrestrial plants, and in those which are aquatic the reproductive organs are, as a rule, out of the water, while cryptogams, or rather that particular portion of the cryptogamic plant which bears the sexual organs, is aquatic or semi-aquatic in habitat. Obviously fertilization in the phanerogams by means of motile spermatozoids is impossible in a medium, such as air, which is not sufficiently dense to allow of their being maintained in it; and it becomes necessary that other methods of locomotion shall be adopted, and the generative nuclei protected, until their destination is safely reached, hence the loss of active powers of locomotion, as that by means of the pollen-tube was adopted.

If the interpretation of the structures we are considering is correct; if the higher form of structure is but a modified form of the lower; and if the one once possessed the same essential organization as the

other, and has reached its higher grade by suppression and modification of parts, we may ask: But is there no connecting link between the two? Is there nowhere among plants a single instance showing the transition? And if we are of a logical disposition, we shall test our inductive conclusions by a deductive premise, and assert that, if the interpretations above given are correct, then we ought to find a transitional form which should exhibit these characters. Inasmuch as the transition from the aquatic to the aërial method of fertilization would involve as a primary factor some modification ensured to protect the essential elements, i. e. the spermatozoids, we should expect to find the microspore remaining intact until the last moment—until it had actually reached the female organ. But having reached it, it would be necessary to liberate the spermatozoids, and to liberate them as near as possible to the ovum; hence we may infer that the microspore would open at the surface directed towards the egg, and, moreover, if a definite direction could be given to the spermatozoids towards the egg, obviously the chances of fertilization would be greater and the risk of accidents less. Thus would arise a pollen-tube that, from the closeness to the egg-apparatus which in the lower flowering plants (*Gymnosperms*) the pollen grains are brought, would be short. But the pollen-tube would be formed only very late in the life of the microspore, and hence the spermatozoids themselves would only develop their locomotor apparatus at a correspondingly late period; in other words, this particular portion of the spermatozoid would be retarded in development. Hence we should expect that the transitional form would exhibit a microspore with a very short pollen-tube and late developed spermatozoids. Is there such a form?

Quite recently (1897) two Japanese investigators, Dr. Hirase and Professor Ikeno, have discovered in the pollen grains of *Cycas revoluta* and *Gingko biloba*—two plants which are placed at the bottom of the phanerogamic scale, and are the most ancient and primitive of gymnosperms—indubitable spermatozoids. The pollen-tube, which is very short and does not reach the archegonia, as it does in *Pinus*, develops at first just like any ordinary pollen-tube, and contains two generative nuclei. But when these have travelled to the bottom of the rudimentary pollen-tube they differentiate into spermatozoids, by the formation of a tuft of cilia at the narrow end of the nucleus. As has just been stated the pollen-tubes do not reach the archegonia, so that when the spermatozoids are liberated they have still some intervening distance to travel. In order that they may do this, the lips of the

micropyle, which close after pollination has been effected, secrete a watery fluid in which the pollen grains lie, and through which at the appropriate moment the spermatozoids may travel.

Thus, in these two plants, the pollen grains, in virtue of a rudimentary pollen-tube, foreshadow the siphonogamous mode of fertilization of the phanerogams, but in virtue of the presence of the spermatozoids still retain the typical zoidogamous mode of the cryptogams. Thus these structures possess characters which respectively distinguish both the phanerogams and cryptogams, and, therefore, constitute a typical connecting link between the flowering and flowerless plants. That the transition from the one mode of fertilization to that of the other has been attained in the phanerogams as a whole, and is being attained in these two lowly gymnosperms, by the disappearance of certain old structures and the development of new, is very well illustrated by this epoch-making discovery, in which the ultimate disappearance of the cilia is foreshadowed by their retarded development, and the appearance of a new structure by the presence of the rudimentary pollen-tube. Moreover, the secretion of water by the lips of the micropyle illustrates in a simple manner the methods by which plants can adapt themselves to new conditions. For *Cycas* and *Gingko* are discarding the aquatic conditions that were necessary for fertilization among their ancestors, but they have not quite fully adapted themselves to the new conditions in the sense that the higher phanerogams have. And since it is obviously risky to leave fertilization to the presence of chance water from a rain-shower, and which, moreover, must coincide with the moment of liberation of the spermatozoids, the plant itself has provided means to ensure the presence of water at the moment when it is most required, and in this way adapts itself to the peculiar exigencies of its transitional stage. The higher phanerogams have carried this adaptation to a greater perfection, and have rendered the act of fertilization independent of the presence of water, which is, at best, a precarious mode in aëro-terrestrial plants, where it is conceivable that, under certain conditions, it may be evaporated at a greater rate than the plant can form it.

The student must not gather from the foregoing remarks that plants have deliberately or intelligently adapted themselves to altered conditions, but that in the course of evolution some plants have varied, and these structural variations have adapted the plants to their environmental conditions, while those which have not so varied have not thus been adapted. In consequence, the one flourishes and is per-

petuated, while the other does not survive in the struggle for existence. It is a matter of the 'survival of the fittest.'

(B.) Development of the Embryo.

The first result to follow the fertilization of the ovum or **oosphere**, called oospore after fertilization, is that it surrounds itself with a thin cell-wall. The primary object of this is, doubtless, to prevent the entry of a second spermatozoid, which tends either to produce a monstrosity or a weakling in the resultant embryo. Most fertilized eggs in animals and plants adopt some method apparently designed for this purpose.

After the formation of the cell-wall segmentation commences. The oospore divides by a median wall in a plane at right angles to the axis of the archegonium (thus differing from ferns, in which it is in the same plane); the upper cell, or one nearest the neck, then elongates and undergoes a few cell-divisions and forms the **suspensor** (Fig. 104, S), while the lower one gives origin to the embryo. This is the first time, in ascending the cryptogamic scale, that we find a suspensor, but its presence is constant in all phanerogams; *Selaginella* thus once more foreshadows an approach to the phanerogamic structure. In the embryonic cell two oblique walls are formed by which three cells are cut off: of these the lowest and median one is the two-edged apical cell of the stem, while the two upper lateral ones give origin by further cell-divisions to the two cotyledons, or the two first formed leaves. The apical cell cuts off segments, alternately right and left, that divide and give rise to a mass of tissue, the central portion of which forms the procambial strand, from which the vascular bundles are developed, and the peripheral portion to the cortex and epidermis. Meanwhile, however, above the lower (right) cotyledon a swelling is produced, called the **foot** (Fig. 104, F), which projects into the tissue of the prothallium, and extracts from it such nutritive material as it may contain, and subsequently passes it on to the growing embryo. The foot is thus an absorbent organ. The first root (R) does not arise until a considerable time afterwards, when it appears in a lateral position between the foot and suspensor; its apical cell arises from one of the deeper cells derived from the segment that forms the lower cotyledon. Owing to the rapid development of the foot the stem is bent upwards, so that the stem and root do not lie on a straight axis but on a curved one.

All the rudiments of the embryo are now present ; the different parts grow, new leaves are formed in the same way as at the apex of the adult plant, each bearing a ligule, and gradually there emerges from the macrospore a young plant, with an obvious resemblance to the parent.

(C.) The Development of the Sporangia.

The early stages in the development of the macro- and microspores are the same, and we may therefore describe them together up to the stage at which they begin to diverge.

A sporangium arises just behind the growing point of the reproductive branch, as a small group of merismatic cells which project from the surface of the stem a little way above the axil of the leaf next below ; sometimes this group of cells arises in the axil of the leaf. But whatever its original position, it always ultimately comes to be borne upon the leaf. At a very early stage this group of merismatic cells becomes differentiated into a peripheral portion of three layers and a central mass of cells which are closely packed, rich in protoplasm, and with large nuclei ; the central group is called the **archesporium**, because each cell of which it is composed is a spore mother-cell. Of the peripheral layers, the two outer ones form the permanent wall of the sporangium and the inner one a nutritive layer called the **tapetum**, which though it persists in *Selaginella* for some time after the spores are formed, ultimately disorganizes into a mucilaginous mass. At a later stage, owing to the growth of the sporangium, the archesporial cells become separated from one another, and assume a spherical form ; these are now called the **spore mother-cells.** From this stage onwards the macrosporangium and microsporangium develop differently. We will consider first the further development of the latter.

Each spore mother-cell divides into four cells which are tetrahedrally arranged, and each of which is a microspore. At first the microspores remain attached together in groups of four, but later they separate from one another. At this stage we may leave them, for their development has reached that point at which we commenced our study of them (supra, p. 174).

In the case of the macrosporangium, only one of the spore mother-cells divides, all the others ultimately undergoing disorganization and forming a food material for the successful mother-cell. This cell

divides, just like any one of the microspore mother-cells, into four cells tetrahedrally arranged. But each of these grows enormously, and so also does the sporangium itself, the four macrospores living upon the disorganized remains of the aborted spore mother-cells. Their outer wall becomes very much thickened, cuticularized, and spiny. Not unfrequently some of the other spore mother-cells divide, but the resulting spores do not attain the dimensions or vigour of those destined to become the four functional spores.

A comparison of the early developmental stages of the sporangia of *Selaginella* with those of the pollen-sacs and ovules of phanerogams will show that there is a close similarity between them (supra, pp. 127 and 131). This may be more easily seen if the successive stages in either case are arranged in parallel columns, as on the opposite page.

The facts thus arranged show very clearly that the nucellus and the embryo-sac of the ovule of the phanerogam are the morphological equivalents of the macrosporangium and the macrospore respectively of the cryptogam, and since they are also physiologically equivalent, inasmuch as they perform the same function—that of reproduction—they are called **homologous organs**.

The principal difference that exists is the development of four macrospores in *Selaginella* and only one embryo-sac in the phanerogams. But as indicated in the last comparison at the bottom of the tabulated columns (p. 187), some gymnosperms and a few angiosperms develop four or more embryo-sacs by the division into four of the archesporial cell. Hence we must regard the embryo-sac as equivalent not so much to a macrospore as to a macrospore mother-cell. In the majority of phanerogams the mother-cell remains at that stage, and only exceptionally divides into four; while in the cryptogams the division into four is the normal event.

(D.) The Life-history and Alternation of Generations.

If we now briefly review the principal events in the life-history of the plant we find that they consist of these: the *Selaginella* plant gives rise by purely asexual processes to two kinds of reproductive bodies, the micro- and macrospores. The former leaves the parent plant while it is yet a unicellular body, and germinates upon the damp soil; the process of germination consists of the formation of what we have seen reason to regard as a male prothallium and antheridium, bearing the ultimate male elements—the spermatozoids.

Phanerogam.		Cryptogam. (*Selaginella.*)
Angiosperm.	Gymnosperm.	
POLLEN-SAC.	POLLEN-SAC.	MICROSPORANGIUM.
Each pollen-sac arises from a group of merismatic cells at each of the four angles of the staminal leaf (anther).	Each pollen-sac arises from a group of merismatic cells on the under surface of the staminal leaf.	Each microsporangium arises from a group of merismatic cells on the stem, near the axil of a leaf and sometimes in the axil, but it always becomes transferred to the leaf.
Each merismatic group forms a central archesporium and a peripheral tapetum; the whole invested by an outer wall.	In each group is a central *single* archesporial cell, with a peripheral tapetum; the whole invested by an outer wall.	In the group is a central archesporium and a peripheral tapetum; the whole invested by an outer wall.
The tapetal cells disorganize and form a mucilage upon which the pollen mother-cells develop.	The archesporium divides repeatedly and forms pollen mother-cells.	The tapetal cells disorganize and form a mucilage upon which the pollen mother-cells develop.	The archesporial cell divides repeatedly and forms pollen mother-cells.	The tapetal layer persists longer than in phanerogams, but ultimately disorganizes.	The archesporium divides repeatedly and forms spore mother-cells.
	Each pollen mother-cell divides into four pollen grains.		Each pollen mother-cell divides into four pollen grains.		Each spore mother-cell divides into four microspores.
NUCELLUS OF OVULE	NUCELLUS OF OVULE	MACROSPORANGIUM
Arises as a group of cells from the thickened margin (placenta) of carpellary leaf (sporophyll).	Arises as a group of cells from upper surface of ovuliferous scale (enlarged placenta) situated in axil of carpellary leaf (sporophyll).	Arises as a group of cells on the stem near axil and sometimes in axil of a leaf (sporophyll).
Each group contains a single archesporial cell, and two cells derived from it (=?vestigial tapetum) which disorganize.	Each group contains a single archesporial cell, and a tapetum derived from it.	Each group contains a central archesporium and a peripheral tapetum in part derived from archesporium.
From the archesporial cell the embryo-sac arises.	From the archesporial cell the embryo-sac arises.	From the archesporium arises a macrospore mother-cell.
In the wallflower, several (4–6) embryo-sacs arise from the archesporium. (Cf. *Selaginella.*)	In some gymnosperms four embryo-sacs arise from the archesporium. (Cf. *Selaginella.*)	From the macrospore mother-cell arise the four macrospores.

We saw that in the lower cryptogams the male prothallium was an independent plant, living a free existence and bearing the male sexual organs; hence we must regard the germinating microspore of *Selaginella* as a free living (independent of the parent plant) sexual-organ-bearing plant, though in a reduced condition.

The macrospore remains in connexion with the parent plant for a considerable period, or rather it attains a correspondingly greater advance in development than the microspore, before it is cast off. At the period when it leaves the parent, or very soon afterwards, it has the structure of an independent plant, and is enabled to live by its own activity in virtue of the chlorophyll which develops in the cells of the prothallium; the prothallium bears the female sexual organs, and though it never leaves the spore, it must, by comparison with lower cryptogams, be regarded as a perfectly independent sexual-organ-bearing plant.

The fertilization of the ovum of the female prothallium by the spermatozoids of the male prothallium ultimately gives rise to an embryo which grows into a *Selaginella* plant. This latter in its turn produces microspores and macrospores, and from them another embryo will arise, which will become a *Selaginella* plant.

Thus the life-history consists of two quite independently living plants called 'generations,' of which the *Selaginella* plant is the **asexual spore-bearing generation**, and the prothallium the **sexual organ-bearing generation.** Hence we speak of the *Selaginella* plant as the **sporophyte**, and of its place in the life-history as the **sporophyte generation**; and of the prothallium as the oophyte, or better and more correctly, as the **gametophyte**, and of its position in the life-cycle as the **gametophyte generation**[1]. Thus the life-history of *Selaginella* consists of an alternation of asexual and sexual generations, or in other words, of the sporophyte and gametophyte. This phenomenon, markedly developed in vascular cryptogams, present but masked in phanerogams, is called '**Alternation of Generations.**' And it is worthy of notice that the gametophyte generation is essentially aquatic, for neither the prothallium can live nor the act of fertilization be possible except under aquatic conditions; while the sporophyte possesses all the characters and the habits of a terrestrial plant,

[1] Both generations are really spore-bearing, but in the sporophyte generation the spores are asexual, and in the gametophyte generation they are sexual, i. e. ova or oospores and spermatozoids.

though preferring moist and shady situations. And since there is reason to believe that the first plants to inhabit the surface of the globe were aquatic, it is conceivable that the first terrestrial plants arose from an aquatic ancestor, as a semi-terrestrial generation in the life-cycle of an aquatic plant, and that once it had originated, some of its descendants became more and more adapted to terrestrial conditions. And we can further conceive that as the terrestrial, sporophyte generation became more permanently fixed and more adapted to a wholly terrestrial life, that the sexual, aquatic generation became correspondingly more an appendage of the sporophyte ; that it gradually lost its independence, and becoming permanently attached to the sporophyte at last depended wholly upon it for its sustenance. Such a condition we see in *Pinus* and all phanerogams, where the endosperm, which is the homologue of the prothallium, does not leave the sporophyte until the seed is ripe, i. e. until another sporophyte (embryo) has been formed. And it will be remembered (supra, p. 175) we emphasized the fact that the germination of the macrospore of *Selaginella* reaches an advanced stage before it leaves the sporophyte ; whereas in the lower vascular cryptogams germination does not even commence until the spores have left the parent plant, so that the gametophyte generation is independent of the sporophyte from the beginning. Thus *Selaginella*, in virtue of this retention of the macrospore and the partially developed gametophyte upon the sporophyte, foreshadows that closer connexion and relegation of an independent gametophyte to the condition of a mere appendage which is such a marked character of the phanerogams or flowering plants.

Hence, in many respects—in virtue of its geological antiquity and its relationship to extinct forms, and of its unique position as a cryptogamic harbinger of a phanerogamic flora—*Selaginella* is second to none, though it may be equalled by others, in its interest to students of botanical philosophy.

CHAPTER XI

THE MALE FERN (*Aspidium Filix-Mas*) and the BRACKEN FERN (*Pteris aquilina*)

1. External Characters.

(A.) The Sporophyte or Fern-plant.

In all the essential features of their organization these two ferns are similar, but they differ considerably in their habit.

The bracken fern may be found on exposed heaths and moorlands, in shady and well-watered valleys, and along the banks of water-courses; on the exposed heaths it seldom attains a large stature, not more than two or three feet in height, but in shady and damp positions it may often attain a height of six to eight feet. The male fern, on the other hand, is never found on heaths or moors, but only under shady hedges and in damp positions. The height to which it may attain varies with the nature of its immediate surroundings, reaching its greatest height on the banks or in the beds of shaded water-courses.

Both are characterized by the possession of an underground stem or rhizome, which in *Pteris* is a long structure (Fig. 106, R), the precise length of which varies with the age of the plant, and which appears to creep horizontally along by means of apical growth, beneath the surface of the ground; upon it, just behind its apex, is borne a single leaf (L), which rises vertically from it. In *Aspidium* (Figs. 107 and 108, I, R) the rhizome is a short, stumpy, roughly conical structure, obliquely set in the ground, and bearing at its summit a magnificent crown of leaves, two feet or so in length.

If we carefully dig up from beneath the ground a complete rhizome of *Pteris* (Fig. 106, R), we shall find that it possesses only one functional leaf (L), situated a little way behind the colourless apex; this is the leaf of the current year. Behind it, at intervals along the dark brown rhizome, there are the basal portions of the leaves of previous years (L^1, L^2, L^3), one for each year; frequently as many as six or eight may be counted, the last more decayed than the first, and behind it the rhizome itself in a decayed condition. At the apical region in front of the leaf of the current year there may be seen a very small leaf, curled up like the handle of a shepherd's crozier, in the bud condition

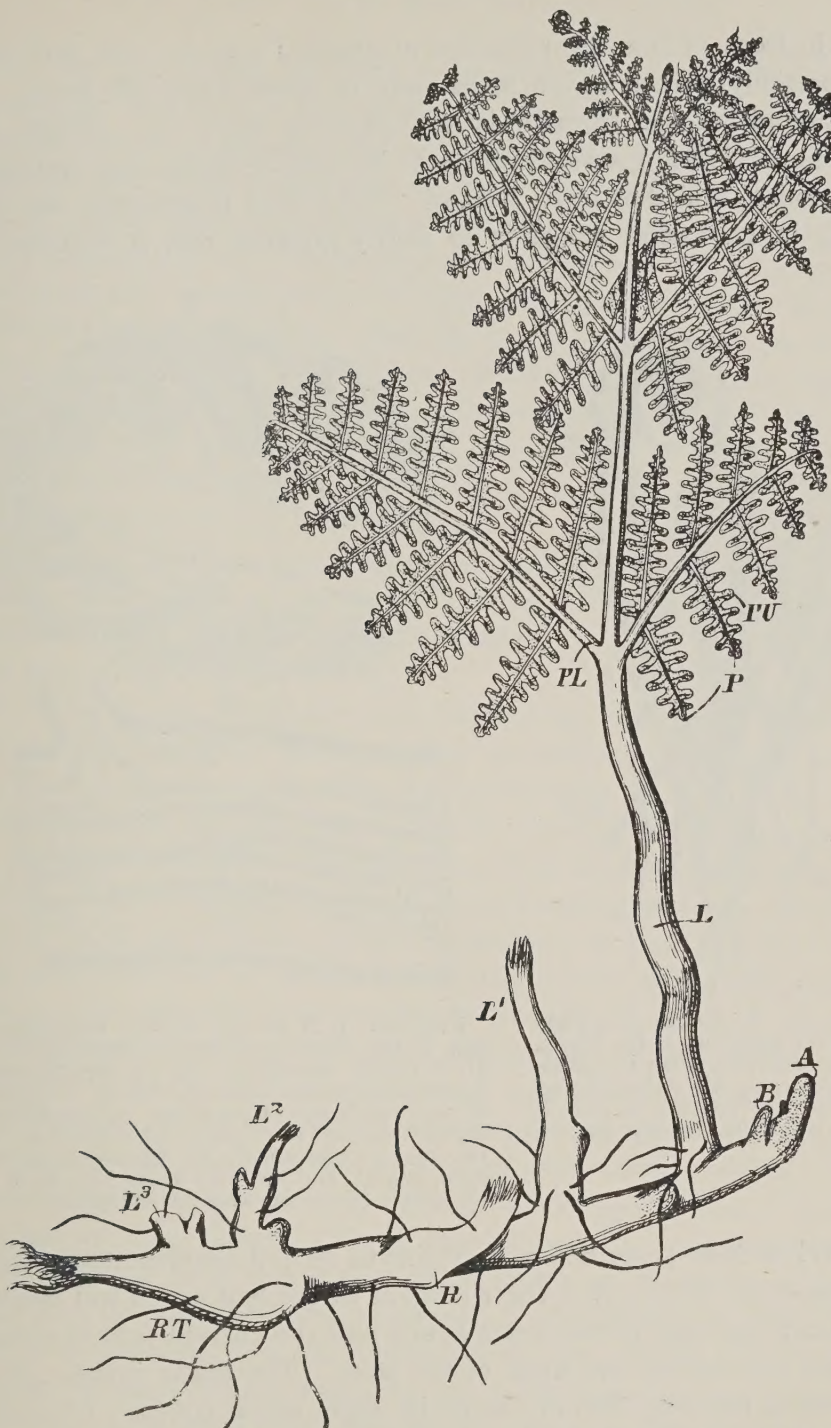


FIG. 106. A plant of the Bracken Fern (*Pteris aquilina*), showing the general habit and structure. A=apex of rhizome; B=leaf-bud of next year's leaf; L=leaf of the current year; L^1, L^2, L^3=decayed bases of past years' leaves; P=pinnæ; PL=petiole; PU=pinnule; R=rhizome; RT=root.

(B) ; in front of this the rudiment of another may be seen, and both are partially hidden by an investment of white, scale-like hairs. At the summit of the rhizome is the growing apex (A). Hence the rhizome of *Pteris* grows forwards at its apex, beneath the surface of the ground, and dies away behind. Each year it produces one leaf, which in its earlier stages is so slowly growing that it occupies an

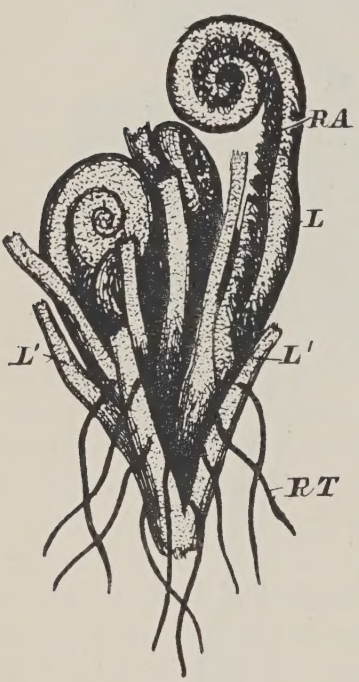


FIG. 107. A plant of *Aspidium* before the unfolding of the leaves. L=leaf of current year; L'=leaves of past years; RA=ramentæ; RT =roots. The rhizome or stem is hidden by the closely packed leaves.

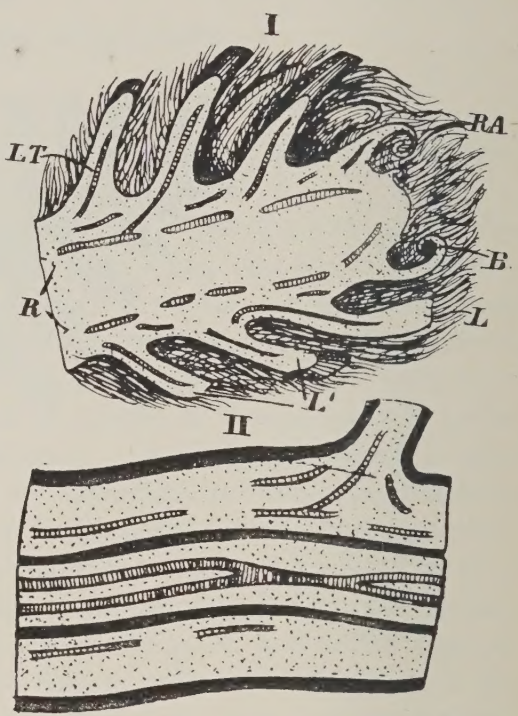


FIG. 108. I. A median section, longitudinally cut, of the rhizome of *Aspidium* (natural size). II. A similar section of a part of the rhizome of *Pteris* (enlarged one and a half times). B=leaf-bud of next year's leaf; L=leaf-base of current year; L'=leaf-bases of past years; LT=leaf-trace; R= rhizome; RA=ramentæ. The vascular bundles are cross stipled, and the solid black strands in the rhizome of *Pteris* represent sclerenchyma.

interval of three years before it attains to its full development ; this is evident from the fact that the rudiment of the leaf which will become the functional leaf in two years hence plus the current year is already present just behind the apex of the stem. The lower surface of the rhizome is flat (Fig. 109, II), while its upper one is convex ; its surface is composed of a very hard dark substance (S), which protects a pulpy, whitish, internal mass. The roots (Fig. 106, RT) arise at any portion of the surface of the rhizome, and very frequently from the basal rem-

nants of the past leaves; they are thus adventitious. In colour they are brownish, and in form filamentous, and they seldom branch.

The rhizome of *Aspidium* (Figs. 107, 108, I) is hidden along almost its whole length by the closely packed basal portions of previous years' leaves (L′), from which the profusely branched adventitious roots (RT) arise in large numbers. The uppermost of these whorls of leaves (L) are those of the current year, and within this whorl are those of next year (B) in the bud-condition, curled up in the same fashion as those of *Pteris*. This particular arrangement of the leaves in the bud, called **circinate vernation**, is very characteristic of the ferns. Within the leaves of the next year are the rudiments of those of the year afterwards; hence in *Aspidium*, as in *Pteris*, each leaf occupies three years in attaining its full development.

The rhizome of *Pteris* forms branches at its apex, while the apex of *Aspidium* does not branch at all: in the latter the branches arise in a peculiar manner from the bases of the leaves, as is the case in ferns having erect stems, i. e. tree-ferns.

The leaves of both *Aspidium* and *Pteris* (Fig. 106) are compound, i. e. the lamina is divided into a number of leaflets called **pinnæ** (P), which are laterally arranged along the petiole (PL). The leaf is thus pinnately divided, and each pinna is also divided into a number of small segments. In *Pteris* the segments are so deeply constricted, that each one forms a small leaflet (PU), and each pinna thus consists of a number of small leaflets called **pinnules**; so that in *Pteris* the leaf is bipinnate, and in some of the lower pinnæ may even be tripinnate, i. e. the pinnules again pinnately divided.

Upon the under surface, and along the margins of the pinnules in *Pteris*, there may be seen in spring and summer a delicate, silver-white membrane, with a hairy-like inner margin; this is the **indusium**, and it covers and protects the developing reproductive bodies. In late summer and autumn this membrane withers and reveals a dark-brown line of dusty bodies, which previously had been concealed beneath it; each little body is a **sporangium** or **spore-case**, and contains sixty-four spores. The aggregate of sporangia with the indusium is called a **sorus**, and the position, form, &c., of the sorus is an important character serving to distinguish the different genera of ferns. In *Pteris* it is marginal upon the under surface of the leaf, but in *Aspidium* the sori are circular patches situated upon the lateral veins of each segment, and are covered by a kidney-shaped indusium.

The petiole or rachis of the leaf (PL), both in *Aspidium* and *Pteris*,

is covered with brown, scarious, scale-like hairs called **ramentæ** (Fig. 107, RA); sometimes they extend along the larger veins of the pinnæ. The ramentæ are chiefly functional in protecting the young developing leaf-buds from undue evaporation and from the cold of winter.

(B.) The Gametophyte or Sexual Plant.

If we examine the surface of the ground where ferns are growing in abundance, so that the soil beneath them is shaded and moist, we shall find a number of little, more or less heart-shaped, green, leaf-like plates about $\frac{1}{8}$ or $\frac{1}{4}$ of an inch long in their longest axis; these are the sexual plants, called **prothallia** (Fig. 118), and they live a perfectly free and independent existence. Like the prothallia of *Selaginella*, they are derived from spores. They may be very easily cultivated artificially by sowing some of the spores upon damp cork in a shady position, preferably the shade cast by fern or other plants. Each prothallium possesses root-hairs (RT) upon its under surface, which penetrate the soil and obtain water and mineral matter (nitrates) from it; the carbonaceous portion of the food is derived from the CO_2 of the atmosphere by means of the chlorophyll contained in the cells of the prothallium, just as in ordinary green plants. Hidden among the root-hairs are the female reproductive organs, the **archegonia** (AR) (in the prothallium figured the root-hairs in this region had not developed); the male organs or **antheridia** (AN) may occur on almost any part of the same prothallium, but are usually confined to the marginal parts of the under surface. Very frequently, however, the archegonia are found on one prothallium, and the antheridia on another, so that there exists a tendency to the production of unisexual prothallia, such as is normally the case in *Selaginella.*

Upon some of the prothallia, very small ferns may be seen, growing up from beneath their under surfaces; these have resulted from the fertilization of the ova of the archegonia. Hence in the fern there is a very distinct 'alternation of generations,' the sexual plant living a perfectly independent existence, since it is capable of obtaining its own food-material. In virtue of the greater distinction between the two generations, the fern-plant does not approach so near to the phanerogamic condition as *Selaginella.*

2. Internal Structure.

(A.) Minute Structure of the Rhizome.

The vascular strands or steles of *Aspidium* are arranged in the form of a perforated cylinder (Figs. 109 and 110, V), each perforation (Fig. 110, FG) of which corresponds in position to the insertion of a leaf upon the rhizome, and is hence known as a 'foliar gap.' The vascular strands of the leaves are connected with the steles of the stem along the margins of the foliar gaps, from which small steles arise and pass outwards to the petiole of the leaf inserted opposite to the gap from which they take their origin. Examination of a transverse section (Fig. 109, I) across the stem shows that the principal vascular cylinders or steles occupy a somewhat central position, and are embedded in a mass of soft parenchyma, the extra-stelar ground-tissue. Between the vascular cylinders and the contour of the stem, the leaf-traces (LT) may be seen cut across in all directions.

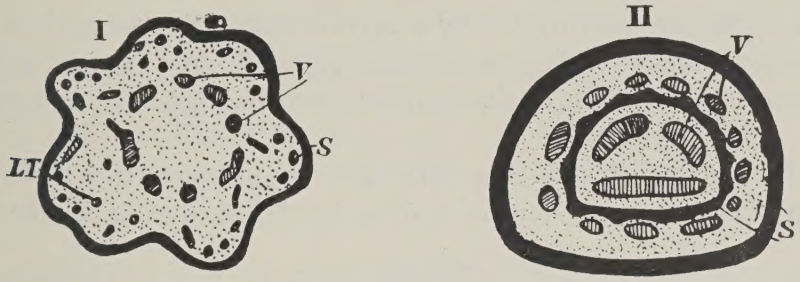


Fig. 109. I. Cut surface of the rhizome of *Aspidium* (natural size). II. Similar preparation of the rhizome of *Pteris* (enlarged one and a half times). LT = leaf-trace; S = sclerenchyma; V = steles.

Fig. 110. A dissection of the rhizome of *Aspidium* in which most of the soft ground-tissue has been scraped away, to show the course of the vascular steles. They are arranged in the form of a perforated cylinder, and the wall of this facing the observer is in black, while the hinder wall away from the observer is in outline. FG = foliar gap; LT = leaf-trace; V = vascular stele.

The contour of such a section is irregular owing to the number of leaf-bases which are cut through. It is limited externally by an ill-defined epidermis, which, morphologically, is not of the same nature as that of phanerogams, and consists of irregularly formed

cells with dark-brown walls ; from it there arise scaly, plate-like hairs. Within is the extra-stelar ground-tissue, composed of parenchyma with cellulose walls, and the cells of which are rich in protoplasm and starch ; the central portion of the ground-tissue contains intercellular spaces, into which spike-like projections of the walls of the cells project, and also glandular hairs, each of which is connected with a single parenchyma cell by a narrow stalk. In the periphery of the ground-tissue is a ring of sclerenchyma (S), composed of prosenchymatous cells, with thick, stratified, brown, lignified, and pitted walls.

Each vascular strand (Fig. 111, EN) is surrounded by its own bundle sheath or endodermis and pericycle, so that each one is a

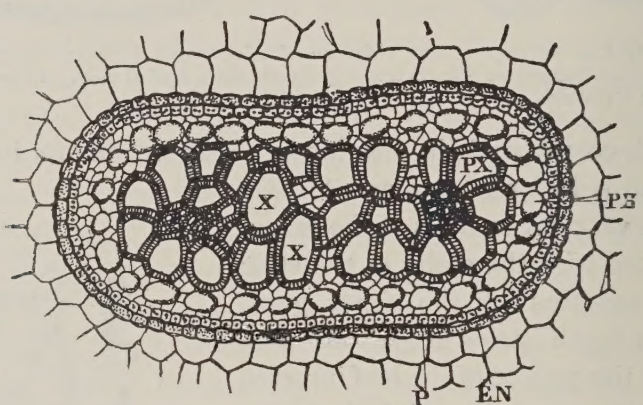


FIG. 111. Transverse section of a stele of *Pteris aquilina*. Magnified 300 times. EN = endodermis ; P = pericycle ; PH = phloem ; PX = protoxylem ; X = xylem.

stele, and the stem is therefore **polystelic**. The endodermis consists of oblong cells with brown contents arranged in the form of a single layer with no intercellular cell-spaces. Within the endodermis is the two-layered pericycle (P) (in *Pteris* it is usually one-layered), consisting of thin-walled cells containing starch. Within this is the layer of phloem, consisting of sieve-tubes of essentially the same nature as those in *Pinus*, i.e. the sieve-plates (Fig. 112, PH) are arranged in groups along the lateral walls ; phloem parenchyma also occurs. In the centre of the stele is the primary xylem (Figs. 111 and 112, X), composed almost exclusively of scalariform tracheides of the same nature as those in *Selaginella* ; situated upon one side of the primary xylem is the protoxylem (PX), which in the smaller steles consists of only one, but in the larger steles of two or more groups of spirally thickened tracheides ; xylem parenchyma

or intra-stelar tissue occurs partly among the tracheides and partly as a ring surrounding the xylem, lying between it and the phloem.

The structure of the rhizome of *Pteris* is in the main similar to that of *Aspidium*, though it differs in certain important details. The steles (Fig. 109, II, v) are arranged somewhat differently, and in a way which may be regarded as roughly forming two concentric circles, of which the inner consists of two or three large central steles, and the outer of several peripheral, smaller ones; from both circles, steles to the leaves are given off. An examination of a transverse or longitudinal section shows that the epidermis (Fig. 112, E) is but a very indistinct one, and that immediately within it is a broad band

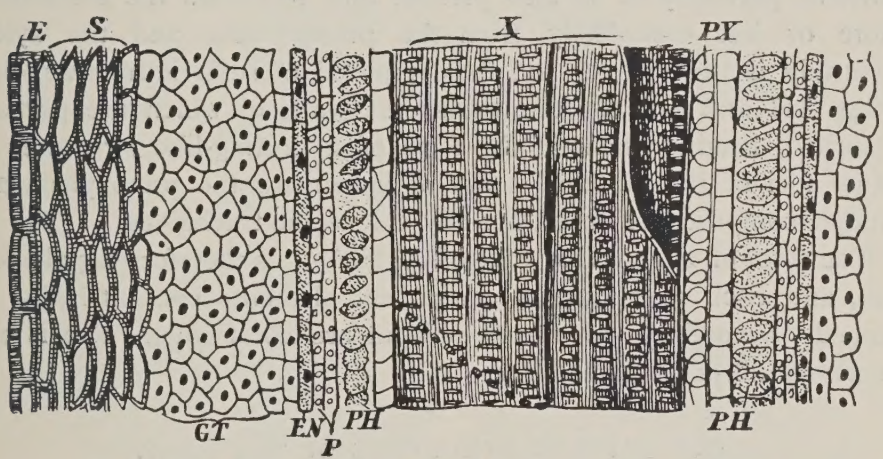


FIG. 112. Longitudinal section of the rhizome of *Pteris aquilina*. Magnified 300 times. E=epidermis; EN=endodermis; GT=ground-tissue (extra-stelar tissue); P=pericycle; PH=phloem; PX=protoxylem; S=sclerenchyma (lignified ground-tissue); X=xylem.

of peripheral sclerenchyma (S), composed of prosenchymatous, thick-walled, and lignified cells. The latter tissue passes gradually into that of the ground-tissue (GT), which is composed of thin-walled parenchyma, with plentiful protoplasm and starch; intercellular spaces are abundant, and into them there project peg-like processes from the cell-walls, which there is reason to believe are composed of various pectic bodies. In the central portion of the ground-tissue there are two dark-brown sclerenchyma strands (Fig. 109, II), the upper one of which is convex and conforms in form to the upper surface of the rhizome, while the lower one is flat. In the semilunar area thus enclosed by them are a variable number of steles, usually two or three, and but rarely one; each stele (Fig. 111) is elliptical in outline and similar in structure to those of *Aspidium*; these steles form the inner circle

mentioned above. In the peripheral portion of the extra-stelar ground-tissue, there are sometimes isolated strands of sclerenchyma, and a ring of small steles which constitute the outer circle of vascular cylinders. Examined in detail, each stele is seen to consist of an outer endodermis (EN), composed of a single layer of brown, oblong cells, within which is the single-layered pericycle (P), composed of oval cells, with thin cellulose walls and starch grains; within this is a layer of small but elongated elements, the lateral walls of which contain sieve-plates, and which probably represents the protophloem. The phloem (Figs. 111 and 112, PH) consists of a ring of much larger sieve-tubes, having essentially the same structure as those of *Pinus* and *Aspidium*; conjunctive parenchyma is also present and separates the sieve-tubes more or less completely from the protophloem and the xylem. Centrally is the primary xylem, composed of scalariform tracheides (Figs. 111 and 112, X), the transverse walls of which are partially absorbed, leaving them in the form of a grating-like structure; at either foci of the elliptical mass of xylem are the protoxylem (PX) groups, composed of small, spirally thickened tracheides.

The stem of *Pteris*, like that of *Aspidium*, is therefore a polystelic one, and each stele has its constituent elements concentrically arranged. Secondary xylem and phloem are not formed; this is true of nearly all cryptogams.

(B.) Minute Structure of the Leaf.

(*a.*) Aspidium.

Several vascular steles pass from the stem through the petiole of the leaf in *Aspidium*, and from these, lateral ones pass outwards to each of the pinnæ; from the midrib of the pinna, lateral ones arise which pass into each of the segments (pinnules), in which they run in the middle line, and give off right and left several small veins which end with a characteristic fork-like mode of branching (Fig. 106). This particular type of venation, which is diagnostic of ferns and does not occur in any other group of plants, is called **the furcate venation.** The vascular strands while running in the petiole are steles of the same nature as those of the stem, but those which pass outwards into the pinnæ have a tendency to become collateral, by the failure of the phloem to completely surround the xylem.

The upper and lower epidermis (Fig. 113, EP) are composed of flattened cells, with sinuous outlines, protoplasmic contents, and

chlorophyll. Stomata (S) are only present in the lower epidermis and consist of two guard-cells (Figs. 113 and 114, G) of the ordinary form, each pair of guard-cells being partially surrounded by a horse-shoe-shaped subsidiary cell (SB). A subsidiary cell, in all cases, is one which has been cut off in the course of development from the same parent cell as the guard-cells (supra, p. 67).

The mesophyll (Fig. 113, M) is not very much differentiated, the upper layers consisting of squarish cells with chlorophyll and small intercellular spaces, and the lower of cells of irregular form, with large intercellular spaces and chlorophyll. An intercellular space always exists immediately over each stoma.

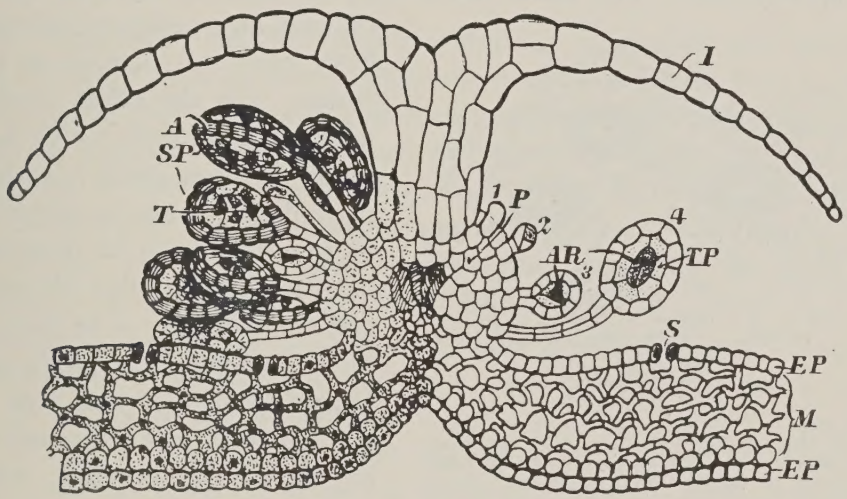


FIG. 113. Median vertical section through a sorus of *Aspidium*. Magnified 300 times. A = annulus; AR = archesporium; EP = epidermis; I = indusium; M = mesophyll; P = placenta; S = stoma; SP = sporangium; T = spore; TP = tapetum; 1, 2, 3, 4 = successive stages in development of a sporangium.

The sori are borne upon a parenchymatous pad, the **placenta** (Fig. 113, P), from the summit of which the membranous, umbrella-like **indusium** (I) arises. From other portions of the placenta there arise stalked bodies, the **sporangia** (SP), each containing sixty-four **spores**. Each sporangium, when mature, consists of a stalk bearing at its free extremity an oval sac or capsule, the walls of which are for the most part composed of very flat cells, of somewhat elongated, polygonal outline; the thin wall thus formed is supported by a single layer of cells, arranged in the form of an incomplete ring and hence called the **annulus** (A), the walls of which become much thickened and suberized and the cells contents disappear. At the incompleted

portion of this ring, the wall of the sporangium is composed of thin-walled, plate-like cells, arranged one above the other, along an axis which is the continuation of that upon which the cells of the annulus are placed. If some mature sporangia are placed upon a microscope slide and gently warmed over a small flame and then quickly examined, it will be found that many of them burst by the formation of a rupture which passes through the surfaces of cohesion of the plate-like cells, and extends irregularly through the thin cells of the wall ; at the same time, it will be obvious that this rupture results from the straightening out of the corky annulus, and that this occurs suddenly, so that the spores are more or less violently ejected from the sporangium. The same result may be attained by substituting for heat, any moisture-extracting body such as alcohol or glycerine. On the other hand, if warmed sporangia which have burst, or those which have been treated with alcohol or glycerine, be breathed upon or immersed in water, the annulus will curve and more or less close the ruptured opening of the spore case. It is obvious, therefore, that the spores are liberated through the drying of the annulus, which tends to contract in the process, and thereby produces a tension in the thin wall, which splits along a plane of least resistance. It follows as the result of this, that in nature the spores will only be liberated in dry weather, when the conditions are favourable for their dispersion ; for if ejected from the spore-case on a wet day, owing to their minute size, they would be intercepted by the first wet body with which they came into contact. The dehiscence of the sporangium in dry weather is an adaptation upon the part of the plant to ensure the wider dispersion of its progeny, and thus in a measure to reduce to a minimum the struggle for a living.

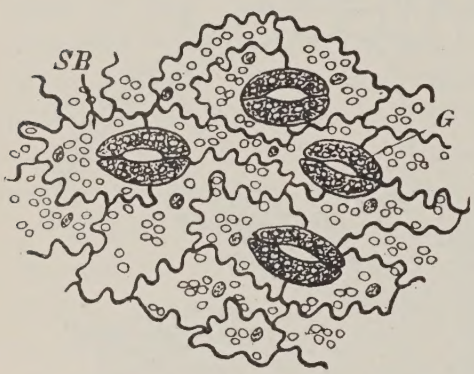


FIG. 114. A piece of the lower epidermis from the leaf of *Aspidium* stripped off and examined in water. Magnified 300 times. G = guard-cells of stoma; SB = horseshoe-shaped subsidiary cell.

Each spore (Fig. 113, T) is a roundish, somewhat trihedral body, with a dark-brownish outer covering, raised into band-like outgrowths. The outer covering is the exospore (Fig. 118, EX) and is cuticularized ; within it is a thin, cellulose endospore (EN) investing a central mass

of protoplasm with a contained nucleus. Each spore is thus a single cell limited by a two-layered cell-wall. All the spores are alike in form, size, and products of germination ; there is no distinction into microspores and macrospores as in *Selaginella*. Hence the fern is **homosporous.**

Some of the sporangia have attached to their stalks little glandular bodies, called **paraphyses** (Fig. 113), of the nature of hairs. It is supposed that they function as organs which take up water in periods of dampness and pass it on to the sporangium in periods of drought.

(*b.*) Development of the Sporangia.

We have seen that in the phanerogams the ovules and anthers, and in *Selaginella* the micro- and macrosporangia, arise from a *group* of cells, and that to this mode of development the term **eusporangiate** may be applied. In the majority of ferns, however, the sporangia (Fig. 113, 1) arise from a *single superficial cell* of the placenta ; and to this mode of origin the term **leptosporangiate** is applied. The distinction which thus exists between the mode of origin of the sporangia in *Aspidium* and *Pteris*, and *Selaginella* and the phanerogams, is not of great morphological significance, for the leptosporangiate condition is secondary and acquired. The geologically oldest ferns are all eusporangiate, and the transition from this primitive condition to that of the secondarily acquired one is to be seen in *Osmunda* (the so-called flowering fern) and in several tropical ferns, which are neither typically leptosporangiate nor eusporangiate in the origin of their sporangia. The leptosporangiate condition of the majority of ferns must, therefore, be regarded as secondarily acquired from the primitive condition.

The first step in the development of a sporangium (Fig. 113, 1) is the projection of one of the epidermal cells of the placenta, which grows out in the form of a little papilla. This papilla then divides into two cells (Fig. 113, 2) by the formation of a transverse wall, and of these two cells, the lower one elongates and divides several times and forms the stalk, while the upper one becomes the capsule. In the upper cell three oblique walls are formed (2), so that there results a central, pyramidal cell, partially surrounded by three superficial cells. The central cell then cuts off a basal segment (Fig. 113, 3), so that it is now quite central, and is completely surrounded by a single layer of superficial cells ; the central cell is the **archesporium**, and

the outer cells by the formation of anticlinal walls ultimately form the wall of the spore-case. The pyramidal archesporium cuts off successive segments which by further divisions form a layer, two cells deep, around it; this is the **tapetal layer** (4, TP), and the cells of which it is composed ultimately disorganize and form a mucilaginous mass upon which the developing spores live. The archesporial cell divides into sixteen cells, which become spherical, and lie free in the mucilaginous mass of the disorganized tapetum; these cells are the **spore mother-cells**, each of which subsequently divides into four spores, tetrahedrally arranged. At first the wall of the spore is thin, but later it becomes divided into two layers, the inner of which remains thin and forms the endospore, while the outer one becomes cuticularized and thickened and forms the exospore.

(*c.*) PTERIS.

The structure of the lamina of the leaf of *Pteris* is almost identical with that of *Aspidium*; the cells of the upper layers of the mesophyll are somewhat more elongated. Several steles pass out into the rachis (petiole), and they are so grouped that when a somewhat obliquely-transverse cut surface is looked at, they present a more or less fanciful resemblance to an eagle with outspread wings; hence the specific name *aquilina*. The rachis is strengthened by a peripheral band of sclerenchyma situated immediately within the epidermis, and there are also sclerenchymatous strands extending through the ground-tissue in between the bundles. The reason for the presence of such a great quantity of strengthening tissue will be easily appreciated by any one who studies the habit of the leaf. As in *Aspidium*, so in *Pteris*, the vascular strands when they reach the individual pinnules are no longer steles, but have become reduced to a single collateral vascular bundle, surrounded by an endodermis. In the rachis, the steles are of the same nature as those of the stem.

The sporangia are the same in structure as those of *Aspidium*, but they arise from a placenta developed upon the under surface of the leaf, along its margin; they are covered by an indusium which is formed as the continuation of the upper epidermis of the leaf, and which folds round to the under surface.

Thus the chief morphological difference between the two leaves is the position of the sporangia and the indusium.

(C.) Minute Structure of the Root.

In its general structure the root of *Aspidium* is similar to that of the phanerogams. There is an external piliferous layer (Fig. 115, PL) from which root-hairs grow out, investing a cortex, which is differentiated into an outer thin-walled (PA), and an inner thick-walled, sclerenchymatous portion (SS). Within the cortex is the endodermis (EN), composed of a single layer of narrow, rectangular cells, with the

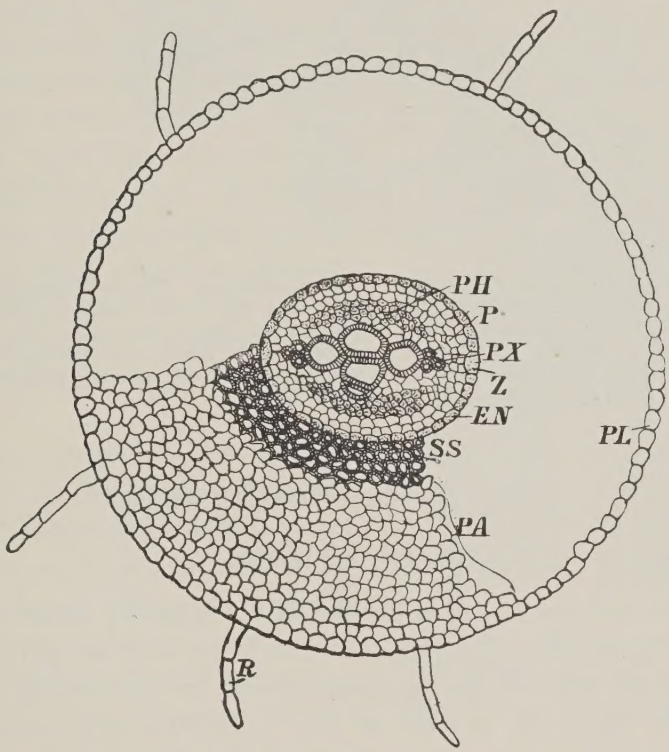


FIG. 115. Transverse section of the root of *Aspidium*. Magnified 300 times. EN=endodermis; P=pericycle; PA=cortical parenchyma; PH=phloem; PL=piliferous layer; PX=protoxylem; R=root-hair; SS=sclerenchyma (lignified inner portion of cortex); Z=rhizogenic cell.

characteristic dot on the radial walls. At two points in the circumference of the endodermis, situated opposite the two protoxylem groups, one or two of the cells are larger than the others; these are called **rhizogenic cells** (Z), and from them the lateral rootlets arise. The pericycle (P) consists of two layers of thin-walled cells. The vascular elements occupy the centre, and are arranged on the usual radial type; the protoxylem (PX) consists of two groups of small, spirally thickened tracheides, and the rest of the primary xylem (X), which is developed centripetally, lies between them, forming

the xylem plate. The primary phloem (PH) lies in between, and therefore alternates with, the primary xylem strands. Between the xylem and phloem there is a little parenchyma. The root is thus a **diarch** one.

The root of *Pteris* is similar to that of *Aspidium*.

Secondary thickening does not occur in any fern.

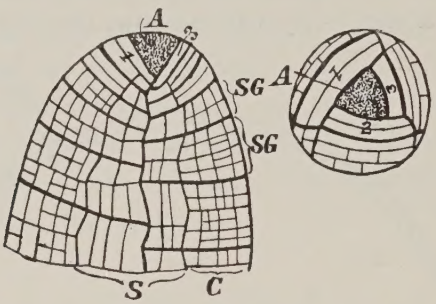


FIG. 116. Apical development in the Fern (*Aspidium*). The left-hand figure represents a median longitudinal section, and the right one a transverse section through the apical cell. A=apical cell; C=outer portion of merismatic tissue from which the cortex (extra-stelar tissue), epidermis, and leaves are developed; S=central portion of merismatic tissue from which the steles develop; SG=segments cut off from apical cell; 1, 2, 3=segments cut off from apical cell and numbered in order.

(D.) APICAL DEVELOPMENT.

(*a*.) RHIZOME.

In *Aspidium* new tissue is formed at the apex by means of a single apical cell (Fig. 116, A), having the form of an inverted pyramid. The three sides of this cell are in contact with the underlying tissue, and from them there are cut off in turn successive segments (1, 2, 3). Each of these segments (SG) grows and divides again repeatedly, and thus there is formed a mass of tissue from which all the organs of the stem arise. We have seen that the rhizome is quite covered by the closely packed leaf-stalks, and the abundance of the leaves is explained by their origin; for each segment cut off from the apical cell, in addition to giving rise to internal tissues, is also the origin of a leaf. The cells cut off by tangential walls from the segments become arranged into a central mass which gives origin to the steles, and into a peripheral mass from which the cortex and epidermis arise.

In *Pteris* the apical cell is not a pyramid in form, but is like one half of a transversely cut biconvex lens, in which the cut surface would correspond to the base of the pyramid. From this cell two segments

only are cut off, alternately right and left. These grow and divide in much the same manner as those in *Aspidium*, though a few of the segments only give origin to leaves.

(*b.*) Root.

The root grows in length by means of an apical cell (Fig. **117**, A), having the form of an inverted pyramid. It is, therefore, similar to the apical cell of the stem of *Aspidium*, but differs from it, in that not only do the three sides cut off segments, but also the base. From the segments derived from the base, the root-cap (RC) arises; this segment grows and divides repeatedly, and ultimately forms a mass of tissue covering the apex of the root, which is replaced behind by the division of the apical cell, as fast as the root-cap wears away, by attrition with the soil, in front.

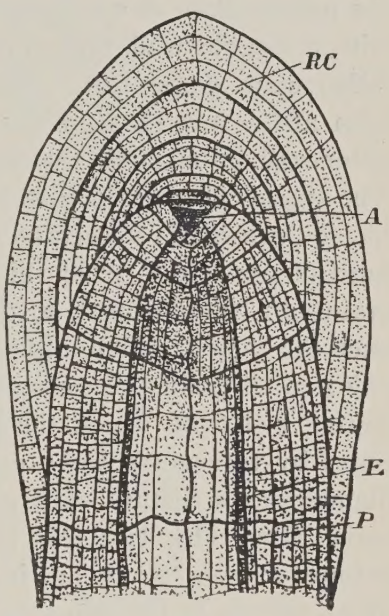


FIG. 117. Median longitudinal section through apex of the root of *Aspidium*. A=apical cell; E=endodermis; P=pericycle; RC=root-cap.

The tissues of the root arise in much the same manner as those in the stem, but only one stele is formed.

Lateral roots arise from the endodermis, and not from the pericycle as in the higher plants. Each rhizogenic cell already described (supra, p. 203) divides by oblique walls and forms a pyramidal cell, which cuts off segments in the same way as the apical cell of the main root. From these segments are derived all the tissues and root-cap of the lateral root. The young rootlet dissolves its way through the cortical tissues of the parent root, by means of a digestive sac which covers its apex, and which is derived from the cells of the inner cortical layers.

The apical cell of the root of *Pteris* is like that of *Aspidium*.

It has already been noted that the roots arise in *Aspidium* from the bases of the leaf-stalks. Their origin within them is very similar to that of a lateral root within the parent root; for each one develops from a rhizogenic cell of the endodermis of one of the steles within the petiole.

In *Pteris* the roots mainly take their origin from the stem near the apex, and arise from rhizogenic cells of the endodermis of the steles in the apical part of the rhizome. When they appear at the base of the leaf-stalk, they do so in the same manner as those in *Aspidium*.

(E.) The Gametophyte or Sexual Plant.

The spores are liberated in dry weather, or in an approximately dry atmosphere, and fall upon the soil at a greater or less distance from the parent-plant or sporophyte. They are at this period single cells with a double wall, and undergo no further change, unless they have fallen upon damp soil. The first indication of germination is to be seen about a week after the liberation of the spore, when the brown outer wall bursts, and the inner one begins to protrude (Fig. 118, I). The single cell then divides into two, and from the outer one a hair-like outgrowth is immediately formed which penetrates the soil and functions as a root (RT); this is the first-formed rhizoid. Chlorophyll grains are then formed, so that from the very beginning of its existence the young gametophyte, by means of its single rhizoid and its chlorophyll grains, can obtain its own food-material. The little projecting cell from which the rhizoid arises, grows and divides several times by transverse walls only, so that there is soon formed a little filamentous structure consisting of cells arranged in a single, linear series (Fig. 118, II); this is the **protonema** (P), a structure which among mosses plays an important part in the life-history of the plant, though in the fern it is not quite such an important one. Very soon, however, the terminal cell of the protonema divides by two oblique walls, thus separating it into three cells, i. e. two lateral, and a median wedge-shaped one (A). The latter is an apical cell, and from it segments are cut off, alternately right and left. From this period onwards, the protonema begins to widen as well as lengthen, and ultimately there is formed a flat, more or less heart-shaped structure, only a single cell in thickness, called the **prothallium** (Fig. 118, III). The apical cell does not always remain such, for it divides into a number of initial cells, all of which contribute to the formation of new tissue; the apical region lies at the base of the depression, and this is due to the more rapid growth of the tissue on either side. As the prothallium grows it also thickens in its middle region (Fig. 119), where it becomes three or four cells thick, and forms a cushion; elsewhere it remains only a single cell in thickness. Upon the cushion at the hinder portion of the under surface of

the prothallium, there arise unicellular hairs, the rhizoids (RT), which penetrate the soil and function as roots.

Arising from the cushion of the prothallium, and situated among the rhizoids, are the archegonia (Fig. 118, III, AR) or female reproductive

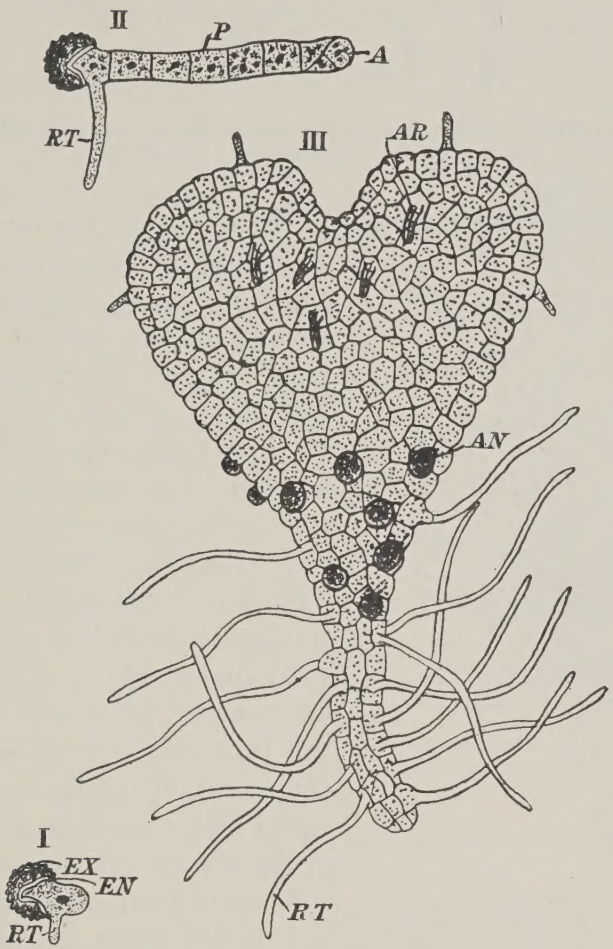


FIG. 118. Germination of the spore of a Fern (*Polypodium*). I. The earliest stage; protrusion of the endospore through the ruptured exospore and formation of the rhizoid. II. Protonemal stage. III. Nearly mature prothallium, seen from the under surface. A = apical cell; AN = antheridia; AR = archegonia; EN = endospore; EX = exospore; P = protonema; RT = rhizoid. Magnified 85 times.

organs. They are very similar to those of *Selaginella*, and have much in common with those of *Pinus*. Each archegonium consists of a neck (Fig. 120, N) of four rows of cells in four tiers, with a neck-canal cell, a ventral-canal cell, and an ovum (O). Each archegonium arises from a single cell of the cushion, which projects a little way beyond the general surface; it then divides by two transverse walls into three

cells, of which the lower (basal) contributes a few cells to the embedded

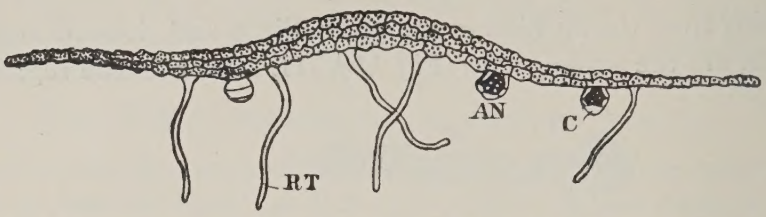


FIG. 119. Transverse section through the antheridial region of a prothallium of *Pteris*. Magnified 80 times. AN = antheridium; C = cap-cell; RT = rhizoid.

venter or base of the archegonium, the second to the ovum and canal cells, and the third to the neck. The third cell grows slightly and then divides, by two vertical walls at right angles to each other, into four column-like cells; each of these then divides by three transverse (horizontal) walls, so that there are now four tiers of cells, each consisting of four cells one above the other; these form the **neck**. The second cell sends out a pointed prolongation which grows into the axial lumen of the neck, and then becomes cut off from the parent cell; this is the **neck-canal cell**. Another cell is cut off and forms the **ventral-canal cell**, and the remaining portion of the second cell becomes spherical, and constitutes the **ovum**. The ovum is a naked mass of granular protoplasm, with a relatively large nucleus; that portion of it which immediately faces the lumen of the neck is clear and without granules, and is known as the receptive spot (Fig. 120, O), since it is at this spot that the spermatozoid enters it. When mature, the neck and ventral canal cells disorganize into a mucilaginous mass (Fig. 120, M) containing malic acid, and the lips of the neck gape open. The neck is not straight, but bends towards the position where the antheridia are as a rule most numerous, i. e. towards the narrow end of the prothallium.

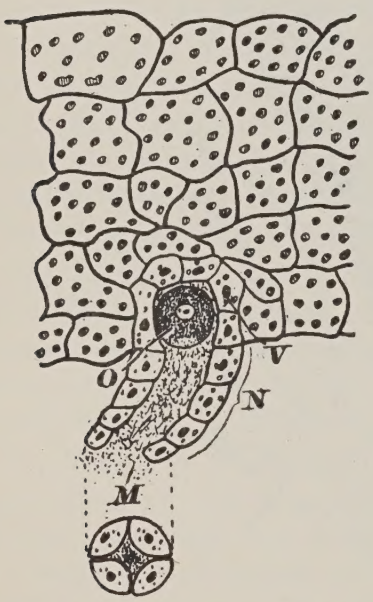


FIG. 120. Transverse section through the cushion of a prothallium passing through an archegonium. M = mucilage derived from disorganization of the ventral and neck canal cells; N = neck; O = ovum; V = venter.

The **antheridia** (Figs. 119 and 121, AN) are borne upon the lateral portions of the prothallium and upon the under surface; sometimes they are situated on the margins, and in more rare instances even on the upper surface. They are hemispherical bodies, composed of two annular cells forming a short, broad tube, and a disc-like covering-cell (C), closing the tube in at its free extremity. When quite mature, the cover-cell is thrown off and the contents of the antheridium liberated. These latter are the **antherozoids** or **spermatozoids** (SP), and when mature each consists of a spirally coiled body (Fig. 121, SP), thicker at one end than at the other, having attached at its thicker end a protoplasmic vesicle (V), and at its thinner, two tufts of cilia. When liberated into the water, the antherozoids swim actively about by the movements of the cilia, always moving with the ciliated end first, and rotating upon their own axis at the same time that they are advancing forwards. Each antheridium arises from a single cell of the prothallium, which bulges out beyond the level of the general surface. The cell then becomes divided into two by a transverse wall, one of which remains within the tissue of the prothallium and forms a pedicel, while the other grows and becomes a semi-globular cell projecting from the surface of the prothallium. The globular cell then divides into two annular cells and a central cell; and a little later the cap or cover-cell is cut off from the outer annular one. Meanwhile, the central cell has been dividing, usually into sixteen cells, which are at first so closely packed that they are polygonal in form, as the result of mutual pressure. In a little time, however, the antheridium becomes larger, and the sixteen cells separate from each other, and become rounded and form cell-walls. These cells are the **antherozoids** or **spermatozoid mother-cells** (Fig. 121, S), and each one gives origin to a **spermatozoid**. They are characterized by the large size of their nuclei, which soon exhibit an alteration of form; it becomes elongated, thickens at one end, and then becomes spirally

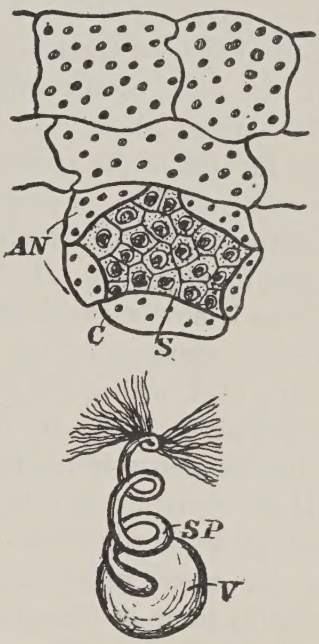


FIG. 121. Transverse section through antheridium of *Pteris*. Magnified 300 times. AN = antheridium; C = cap-cell; S = spermatozoid mother-cells; SP = spermatozoid; V = vesicle.

twisted, forming about three or four coils. At the thin end of the coiled nucleus some of the protoplasm of the cell becomes converted into contractile threads, which become attached to the nucleus and form the cilia. At the other end, another portion of the protoplasm becomes converted into a globular vesicle.

Soon after the spermatozoid mother-cells are liberated into the damp soil, the walls of the cells become dissolved and the spermatozoids swim actively about. In a very short time, they aggregate around the open mouths of the archegonia, become entangled in the slime there liberated, and some begin to wriggle down the neck; one more advanced than the others gains the receptive spot of the ovum and begins to wriggle in. If it has not hitherto lost its vesicle and cilia, it loses it now as soon as it enters the ovum. Almost immediately after the entrance of the spermatozoid into the ovum, the latter surrounds itself with a cell-wall, and thus prevents the entry of a second spermatozoid. The act of fertilization thus consists in the fern, as in all higher plants, of the fusion of the male and female nuclei.

If the spermatozoids be watched under the microscope while swimming about on the under surface of a prothallium turned upside down, and immersed in distilled or rain water, it will be seen that quite suddenly some of them turn aside and swim in a direct line towards the nearest archegonium. Apparently there is some attractive influence that causes the spermatozoid thus to suddenly change its direction. Is the nature of this attraction experimentally ascertainable? If several ripe fern prothalli be washed clean of dirt particles and crushed in a small quantity of distilled water, and filtered, and a little of the filtrate be placed in a very small capillary tube closed at one end[1], upon placing the open end of one of these in a drop of distilled water containing the spermatozoids, it will be found that they crowd round the open orifice of the tube, and some indeed pass up into it. Obviously the filtrate contains something that exercises an attractive influence upon the spermatozoids. A chemical analysis of the filtrate, or a micro-chemical investigation of the slime that oozes out from the mouths of the archegonia, shows that malic acid, a substance that gives to apples their characteristic taste, is present. If, now, the filtrate in the capillary tubes be replaced by a weak solution of malic acid, and the experiment repeated, it will be found that the spermatozoids crowd round the open orifice of the tube. Obviously, then, the attractive

[1] This has to be accomplished by placing the tubes in the filtrate and then placing the whole under an air exhauster.

substance is malic acid. The phenomenon thus presented of a definite chemical substance influencing the direction of a living unit or organism is called **chemiotaxis**, and has already been noticed under its general aspect (supra, p. 179).

As a rule, in both *Aspidium* and *Pteris*, the prothallia contain both antheridia and archegonia. But not infrequently, the archegonia are restricted to one prothallium and the antheridia to another. In such cases the male prothallium is a dwarf one, and has a tendency to form filamentous branches, upon the margins of which the antheridia are borne. The female prothallia are of the normal size and form. In other cases the antheridia are formed first and ripen, and the archegonia are formed upon the same prothallium at a later stage, and are fertilized by the spermatozoids of a younger prothallium.

(F.) Segmentation and Development of the Oospore.

After fertilization, the ovum or oosphere is called the oospore. After the formation of the cell-wall, the first result of fertilization is the division of the oospore into two by a wall (basal wall) parallel to the long axis of the archegonium, and oblique to the plane of the prothallium (Fig. 122, B); this divides the oospore into a hypobasal half (H) directed towards the broad end of the prothallium, and an epibasal half (E) facing the narrow end. The next wall (T, transverse wall) is nearly parallel to the plane of the prothallium, and at right angles to the first; it cuts the two halves into four cells. Another wall (M, median wall) next appears, parallel to the long axis of the archegonium and at right angles to the other two; this divides the whole oospore into eight parts or octants. From these octants arise all the different parts of the sporophyte. From the upper epibasal octants (S) the apex of the stem arises; from the lower epibasal octants the cotyledon or first leaf (C) arises; from the upper hypobasal octants an absorptive and temporary organ, called the **foot** (E),

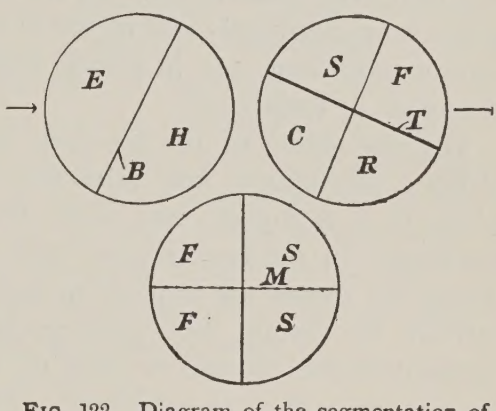


FIG. 122. Diagram of the segmentation of the oospore in a Fern. B = first wall; C = cotyledon octants; E = epibasal half; F = foot octants; H = hypobasal half; M = third wall; R = root octants; S = stem octants; T = second wall. The two top figures are seen in side view and the lowest one is represented as seen from above.

takes its origin; and from the lower hypobasal octants the apex of the root arises.

The cotyledon grows rapidly, and turns upwards from beneath the prothallium, and the root forms a root-cap, and grows downwards into the soil. For some time the stem remains a comparatively insignificant organ, but later there are developed from it several leaves, after which it begins to attain greater size.

(G.) Alternation of Generations and Homologies.

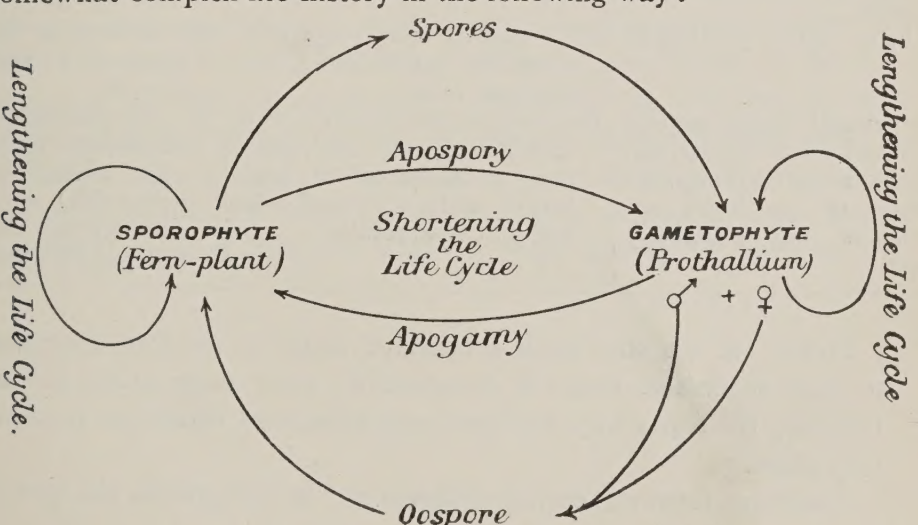
The life-history of the fern thus consists of an alternation of two quite distinct and independent generations: the sexual or **gametophyte** one, and the spore-producing or **sporophyte** one. The gametophyte arises from the germination of the spore, and is in every way an individual plant, of somewhat lowly grade, and adapted to an aquatic mode of life. The sporophyte which arises from the gametophyte is a highly complex and specialized individual, and is adapted to a terrestrial mode of life. In the normal course of events these two generations alternately and regularly succeed one another. But under certain conditions, and in certain ferns, the life-history may be either shortened or lengthened.

The shortening of the life-cycle may occur in one of two ways: either a prothallium may arise directly from the tissues of the fern-plant, or a fern-plant may arise directly from the tissue of a prothallium. In the former case there may be either concurrent sporal arrest (no spores are formed) or not: the prothallia may arise vegetatively by certain cells undergoing division, and these may be situated in the capsule or stalk of arrested sporangia, in the apex, margin, or surface of a pinnule. The dividing cells grow outwards and form either filamentous, protonemal structures, or flattened expansions containing chlorophyll, and upon which functional sexual organs are developed. Such direct development of the gametophyte from the sporophyte has been observed with sporal arrest, i. e. spores were not formed on the plant at all, in *Asplenium Filix-fœmina*, var. *clarissima*, and without sporal arrest, i. e. spores were formed as usual, in certain species of *Trichomanes*. The phenomenon has also been observed in *Polystichum angulare*, var. *pulcherrimum*, and in *Pteris aquilina*. This particular mode of shortening the life-cycle is known as **apospory**, or the short cut from the sporophyte to the gametophyte.

In the other method, that of the short cut from the gametophyte to the sporophyte, and called **apogamy**, a young fern-plant, first of all

the leaf, then the apex of the stem, and last of all the root, arises as a vegetative outgrowth of the tissue of the prothallium. Certain cells, usually situated a little behind the apex, become merismatic and form tracheides and other tissues, from which the young fern-plant arises. This direct development of the sporophyte from the gametophyte may take place with or without the concurrent formation of sexual organs. In *Aspidium Filix-mas*, var. *cristatum*, *Aspidium falcatum*, and *Todea africana*, only antheridia are formed on the prothallia. In *Pteris cretica*, in addition to the antheridia, archegonia are formed, but they never reach maturity. In some cases, apparently normal archegonia are formed, but they do not appear to be capable of fertilization, for they wither and die without developing embryos.

The lengthening of the life-cycle may take place by the interpolation of either a second sporophyte or a second gametophyte into it. In many ferns, notably the cultivated varieties of *Pteris*, young ferns are to be seen growing upon the leaves of the sporophyte. These arise by the formation of an apical cell in the tissue of the leaf, and which by its divisions forms a new sporophyte. The effect of this, in relation to the life-cycle, is the retardation of the formation of the spores, and a consequent lengthening of the cycle. In a precisely analogous way the sexual organs may be retarded by the vegetative reproduction of a gametophyte from a gametophyte. In a fern named *Gymnogramme*, the prothallium branches profusely, and at the extremity of each branch a 'tuber' is formed which penetrates the ground and becomes separated from the parent prothallium; from these new prothallia arise. We may diagrammatically represent this somewhat complex life-history in the following way:



If we now compare the various stages in the formation of the sporangia and sexual reproductive organs of the fern with those of *Selaginella,* we shall find that many homologies exist:

Selaginella.				Fern.	
Microsporangium.		Macrosporangium.		Sporangium.	
Each sporangium arises from a *group* of cells on the stem which subsequently becomes shifted to the leaf.		Each sporangium arises from a *group* of cells on the stem which subsequently becomes shifted to the leaf.		Each sporangium arises from a *single* cell of the placenta on the under surface of the leaf.	
In the group is a central archesporium and a peripheral tapetum; the whole invested by an outer wall.		In the group is a central archesporium and a peripheral tapetum; the whole invested by an outer wall.		The single cell divides and forms a group consisting of a central archesporium, peripheral tapetum, and investing wall.	
The tapetum persists for some time, but ultimately disorganizes.	The archesporium divides repeatedly and forms spore mother-cells.	The tapetum persists for some time, but ultimately disorganizes.	From the archesporium arise macrospore mother-cells.	The tapetum soon disorganizes.	The archesporium divides and forms sixteen spore mother-cells.
	Each spore mother-cell divides into four microspores.		One only of the macrospore mother-cells divides into four macrospores.		Each spore mother-cell forms four spores.
The germination of the spore commences by its division into two cells, a larger and a smaller.		The germination of the spore begins by repeated nuclear division.		The germination of the spore begins by its division into two.	
The little cell = prothallial cell.		At a slightly later stage cell-walls are formed and a prothallium results.		By subsequent and repeated division a prothallium is formed.	
The larger cell divides several times and forms antheridial cells and a central group; by division of the latter antherozoids are ultimately formed.		By enlargement of certain prothallial cells and their division, an archegonium, with ventral and neck canal cells and an ovum, results.		By enlargement and division of certain single prothallial cells, antheridia with spermatozoids, and archegonia with ventral and neck canal cells, and an ovum result.	

Hence we see that each successive stage in the fern corresponds to each successive stage in *Selaginella*; each stage arises in fundamentally the same way, and produces structures which are fundamentally alike.

There are, however, certain differences: in *Selaginella* the sporangia

arise from a group of cells, while in the fern they arise from a single one; this is not an important morphological difference, and it has been already considered. In *Selaginella* we have a distinction into male or microspores, and female or macrospores; in the fern the spores are all alike. The microspores produce very reduced male prothallia which bear the remnants of antheridia and spermatozoids; the macrospores produce female prothallia, fully developed though permanently retained within the spore. The homosporous spores of the fern produce, as a rule, prothallia which bear both male and female organs, though we have seen that in certain instances dwarf male prothallia may arise, and female prothallia of normal dimensions. Hence it would appear that in respect of this, *Selaginella* differs in the main from the fern, in that the sexes have become definitely fixed to separate prothallia; that which arises now and then as a variation in the fern, is the normal order of things in *Selaginella.*

We have already emphasized the independent existence of the gametophyte in the fern; and we have also noticed the restriction of this independence, and the assumption of the first stage of dependence upon the sporophyte, of the gametophyte in *Selaginella.* The fern, in fact, is the first plant which we have met with, in descending the botanical scale of life, which shows an obvious 'alternation of generations.' It is only by comparing the various stages in the life-history of the higher plants with the corresponding stages in that of the fern, that we are able to trace in them the alternation of two generations. As we ascend the scale, the sexual generation suffers progressive reduction, its accessory and unessential parts disappear, and it becomes increasingly an appendage hidden away within the tissues of the sporophyte. And in the flowering plants, to such an extent has this been carried, that without a knowledge of the life-history of the fern, it would be impossible to conceive of such a phenomenon as an 'alternation of generations'; and even with this knowledge, the conception of alternating generations in the higher plants is only possible when the microscopical details of development are worked out and compared stage by stage with those of the fern.

CHAPTER XII

(B.) BRYOPHYTA

THE MOSSES (*Polytrichum commune*).

The Gametophyte.

1. External Characters.

When we pass from the study of the fern and the higher plants to that of the moss, we pass over a big gap in the vegetable kingdom, and we find that the relative arrangement, in respect of their structural characters, of the two generations is quite reversed. In all the plants we have so far studied, the sporophyte is structurally the more complex, and is the larger and more apparent of the two generations; but in the plant we have next to study, the plant-like generation is not the sporophyte but the gametophyte, the sporophyte not having yet attained a higher structural complexity than a simple sac containing spores, and it is, moreover, largely dependent upon the gametophyte for its existence. That which we ordinarily regard as the moss-plant is the gametophyte, and is equivalent to the prothallium of the fern, while the so-called moss-fruit is the sporophyte, and is homologous to the fern-plant.

Polytrichum commune is a common moss in certain localities, inhabiting forests and moorlands. It is among the largest of our British mosses, attaining a height of some six inches or more. Unlike the more common and smaller *Funaria* which grows on stone walls and damp ground, it only sexually reproduces in the spring and early summer; *Funaria* sexually reproduces throughout the year. *Polytrichum* is dicœcious, i.e. the male and female organs are borne upon different plants; most mosses are like this, but some (*Bryum*) are moncœcious. *Polytrichum*, like most mosses, grows in clusters of a great number of individuals, and such is their aggregation that the lower leaves of every individual are brown and scarious, the chlorophyll having disappeared through failure of the light to reach them. Some of the plants possess cup-like rosettes of red or orange leaves at their summits, which enclose and protect the male organs.

Polytrichum possesses a stem bearing leaves, and at its base a number of brown rhizoids but no true roots; roots are absent in all mosses. The leaves are arranged in a spiral with a divergence of $\frac{3}{8}$, i.e. in passing round the stem three times the curve would pass through the bases of eight leaves, before we reached a leaf immediately above the one from which we started; or, the interval between the insertion of any two leaves is $\frac{3}{8}$ths the circumference of the stem. The leaves (Fig. 124, I, B) are inserted by a broad base to the stem, they are in form linear-lanceolate with a broad base, and traversed by a distinct midrib (M), which is, however, only a thickening of the ordinary tissue of the leaf with a slightly differentiated central tissue, there being no true vascular bundles in either the stem or leaves of mosses.

The stem and leaf of the moss are not homologous to the stem and leaf of higher plants, since they belong to a different generation, but at most they are only analogous organs, i.e. serving the same physiological purpose.

2. Internal Structure.

(A.) The Stem.

The structure of the stem of *Polytrichum* is very simple, though not so simple as that of some mosses. Externally (Fig. 123, S) it is limited by a band of prosenchymatous, stratified, and lignified cells; the cell-walls are reddish in colour and so thick that the cell-cavities are almost obliterated. Externally this cylinder of sclerenchyma is covered by a thin cuticle, formed by the alteration of the outer walls of the outermost layer of cells. The sclerenchymatous zone passes gradually into a relatively broad cortex (C), consisting of thin-walled cells, with protoplasm, oil globules, and starch grains. Centrally lies a strand of tissue which may be compared to the vascular bundles of higher plants, since it is slightly differentiated, and probably serves as a conducting channel. It is not distinctly marked off from the cortical zone, and its peripheral portion (P) consists of a small-

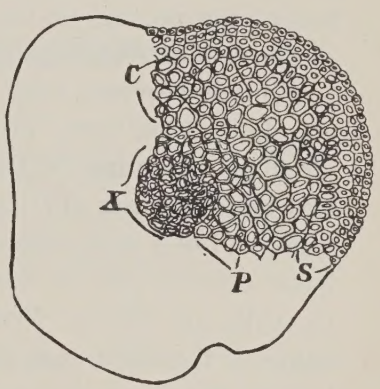


Fig. 123. Transverse section of stem of *Polytrichum commune*. C= cortex; P=functional phloem; S= band of lignified prosenchyma (sclerenchyma); X=functional xylem.

celled tissue, the cells of which are thin-walled and probably composed, not of cellulose, but of some modification of it; this tissue may be compared to the phloem of higher plants, though it is wholly cellular, with unpitted walls and no sieve-plates. Within this, occupying the central axis of the stem, is a thick-walled tissue (X), composed of elongated cells with a tendency to assume a wavy outline, with unpitted walls, and separated from one another by thin septa obliquely arranged; this probably plays the part of the xylem of higher plants.

Here and there in the cortex may be observed small strands similar to the central one: these are the leaf-traces or foliar strands coming in from the leaves and passing towards the central strand.

(B.) The Leaf.

The leaf of *Polytrichum* is somewhat more complex than that of most mosses, and we shall first study a simpler one. The leaf of *Funaria* is composed of a single layer only of parenchymatous cells, uniformly oblong in form, the marginal row of cells being longer and narrower than the others; the cells are crowded with chlorophyll grains. The leaf is traversed by a midrib composed of elongated, brown thin-walled cells, which probably serve to conduct water from the leaves to the stem and vice versa. There is no cuticle, so that the leaves can themselves absorb water; stomata are absent on the leaves, but present on the stem.

The leaf of *Polytrichum* (Fig. 124) is linear-lanceolate in form, with a minutely serrated edge, and expanded at its base (I, B), where it is attached to the stem, into a somewhat rectangular-shaped blade. The detailed structure of the leaf varies at different parts. The basal expanded portion (B) consists of a midrib (M) with several rows of cells, and of a wing-like expansion on either side, made up of a single layer only of cells in thickness; the outer walls (upper and lower) of the cells are thicker than the lateral ones, and all are yellow-red in colour; the cells contain protoplasm and a few chlorophyll grains. The midrib is covered externally by an upper and lower layer of cells, similar to those of the lateral expansions but smaller and thicker walled; in the centre of the midrib is a strand of red-brown coloured cells (III, F), similar to the foliar strands in the cortex of the stem and probably of the nature of a xylem; these are surrounded by a sclerenchymatous tissue (S), the cells of which have very thick walls and no protoplasm. At the junction of the wide basal (I, B) with the narrow

linear-lanceolate portion (L), the lateral wings are less broad and are composed of two layers of cells, while the upper surface of the midrib is traversed in a longitudinal direction by rows (lamellæ) of cells, each row two cells deep, and crowded with chlorophyll granules. The upper portion of the leaf (linear-lanceolate shaped portion, L) is composed of two covering (epidermal?) (Fig. 124, III, E & E′) layers, of which that on the under surface (E′) consists of narrow oblong cells,

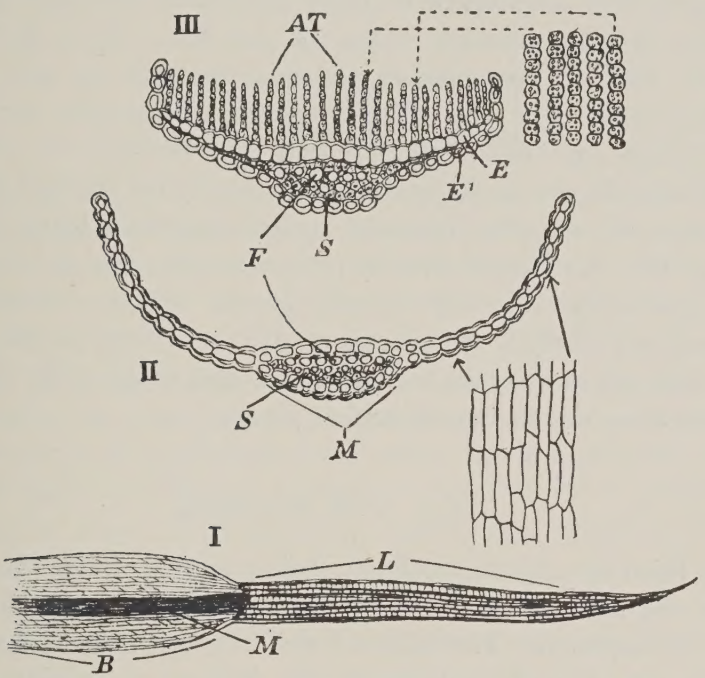


FIG 124. Leaf of *Polytrichum commune*. I. View of upper surface of leaf. Enlarged four times. II. Transverse section of the basal (broader) part of leaf (B); the figure to the right represents a surface view of the leaf. Magnified 300 times. III. Transverse section of the narrow upper portion of leaf (L); the figure to the right represents five of the layers AT drawn on a larger scale. Magnified 300 times. AT=assimilating tissue; B=base of the leaf; E and E′=upper and lower covering layers; F=conducting tissue; L=upper narrow portion of leaf; M=midrib; S=sclerenchyma.

with very thick outer walls, that at either margin of the leaf turns upwards and forms a wall-like structure a single layer of cells in thickness. The upper covering layer (E) consists of squarish cells with uniformly thick walls. In the region of the midrib there are strands of very thick-walled sclerenchyma (S), and the cell cavity of the constituent cells is almost obliterated. In the central portion of the midrib there is a large-celled tissue (F) with colourless walls: it probably represents the upper portions of the foliar strands of the

stem. Extending along the whole of the upper surface of this portion of the leaf are a number of vertical lamellæ (AT), limited on either side by the upturned marginal walls just described; each lamella is a single layer of cells in thickness, and six or seven in vertical height, and is composed of broadly oblong cells with thin walls, except the terminal row of cells which is thicker walled, and all of which are crowded with chlorophyll grains. The lamellæ are laterally independent of each other so that air can pass between them, and in virtue of the abundance of their contained chlorophyll, they are obviously the assimilating tissue of the leaf. Each lamella is so arranged that it corresponds to a single row of the superficial (covering) cells. Fig. 124, III, represents a transverse section of the leaf, in which also the lamellæ are seen transversely cut across. The vertical lamellæ are analogous to the mesophyll of the leaf of flowering plants, and we see that here the assimilating and transpiring tissue (infra, p. 456) is exposed directly to the surface, and is not protected by a second external (epidermal) layer. Thus, *Polytrichum* can transpire very freely if conditions render it necessary, but it can also check transpiration by folding in the lateral wings over the lamellæ, and thus close them in, as in higher plants.

(C.) The Rhizoids.

The rhizoids are multicellular hairs, arising from the superficial cells of the stem. They are divided by oblique septa and grow by apical development. The cells are rich in protoplasm and oil globules. The rhizoids branch very freely, by means of cellular outgrowths from any of the cells forming the stouter branches; these latter in *Polytrichum* coil round one another like the threads in a rope.

(D.) Apical Development.

The stem of *Polytrichum* increases in length by means of an apical cell, which is tetrahedral in form, with its apex inverted. From the three sides of this cell successive segments are cut off, and from each segment there may be derived the tissues of the stem, a leaf and a lateral branch. Each segment when cut off from the apical cell divides into an inner and an outer cell, of which the latter again divides into an upper and a lower cell. The upper cell gives origin to a leaf, and the lower cell to a lateral branch; lateral branches are not,

however, always formed: thus the mosses differ from the plants we have so far studied in that the lateral branches (shoots) arise, not in the axils of the leaves, but beneath them. The inner cells cut off from the primary segments give rise to all the tissues of the stem, except superficial layers which are derived with the leaves and shoots from the outer cells.

Each leaf continues its growth for a limited time by means of a two-sided apical cell, which cuts off segments successively from either side, very similar to that in the prothallium of the fern.

3. Reproduction.

(A.) The Sexual Organs.

The male plants of *Polytrichum*, when ripe, are distinguished by the rosette of purple leaves, called a **perigonium**, at the summit of the stem. These are different to the ordinary lower leaves, being broader and shorter, and laterally expanded at the upper part. They are arranged in a spiral, passing round the apex of the stem, and the **antheridia** (Fig. 125, A) are borne in their axils. By the side of the antheridia, or among them, are metamorphosed, multicellular, glandular hairs of a spathulate form, called the **paraphyses** (P); the function of these is probably to absorb water when it is plentiful and secrete it when scarce, thus ensuring more or less uniform conditions of development for the antheridia. These latter are oval or club-shaped bodies, consisting of a sac, the wall of which is one layer of cells in thickness, supported upon a multicellular stalk or pedicel. Within the sac is a mass of very minute cubical cells, the **spermatozoid mother-cells.** When fully matured, the wall of the sac swells in the presence of moisture, such as a drop of rain water, and pressing upon the mother-cells within, forces them out in one mass, through a rupture in the wall at the apex of the sac. Immersed in water, the mother-cells become mucilaginous, and the metamorphosed nucleus of each one—now called the **spermatozoids**, and which are twisted upon themselves, enlarged at one end, and bearing two cilia at the other—become liberated and find their way to a female 'flower.'

The archegonia (Fig. 125, AR) are borne upon plants which do not possess special leaves, but the ordinary leaves at the apex are closely packed and enclose the female organs in a bud-like structure. As in the male flower, the leaves are arranged on a spiral, and constitute a kind of 'perianth' called the **perichætium.** Paraphyses are

present, but they are in the form of jointed filaments. Each **archegonium** is a flask-shaped organ, consisting of a very long neck (N), of six rows of cells, and a venter (V) having a wall of two layers of cells in thickness, supported upon a multicellular stalk. Along the axis of the neck are a number of canal cells, and within the venter a naked mass of granular protoplasm, the **ovum** (O); between the ovum and the lowest (most ventral) of the canal cells is a ventral-canal cell. At the time of maturation, the ventral and neck canal

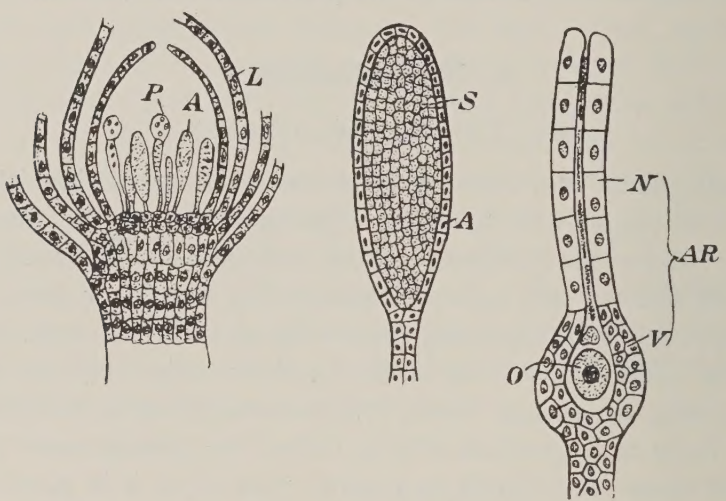


FIG. 125. Sexual reproductive organs of *Polytrichum commune*. Magnified 300 times. The figure to the left represents a median vertical section through the apex of the stem. The middle figure shows a single antheridium, and the figure on the right a single archegonium. A=antheridium; AR=archegonium; L=leaves of perigonium; N=neck of archegonium; O=ovum or oosphere; P=paraphyse; S=spermatozoid mother-cells; V=venter of archegonium.

cells disorganize and form a mass of mucilage, which forces the terminal cells of the neck slightly apart; through the mucilaginous mass the spermatozoids force their way and reach the ovum, which they fertilize. As in the case of the fern, so in that of the moss, it has been experimentally shown that the mucilage exercises an attractive influence for the spermatozoids, in virtue of some chemical substance which it contains; the substance, however, is not malic acid, but cane-sugar.

(B.) Development of the Sexual Organs.

A study of development shows that the morphological nature of the sexual organs is very various: they may be metamorphosed shoots, leaves, trichomes (hairs), or even the metamorphosed apical portion

of the main axis ; in the last instance they arise from the apical cell of the stem, after which the growth of that ceases, but the growth of the stem may be continued by means of a lateral shoot. The sexual organs arise from a single cell, and their morphological nature, therefore, depends upon the position of this cell ; if it arises from the upper cell of the outer half of a segment (supra, p. 220) it represents a metamorphosed leaf; if from the lower cell, a modified shoot ; and if from superficial cells of the stem, modified hairs.

But whatever the morphological position of the parent cell, its development into the mature organ is the same. The mother-cell of an antheridium divides by one or two transverse walls, after which an apical cell is formed, that cuts off two rows of segments. Each segment becomes divided by two tangential walls, in such a way that each segment contains two outer cells and one central one : hence, in a transverse section through a developing antheridium, which passes transversely through the two rows of segments, four outer cells may be seen enclosing two central ones. The central ones by further subdivision give origin to the spermatozoid mother-cells, and the outer ones to the wall of the sac. The first few cells cut off by transverse walls become the stalk.

The mother-cell of an archegonium divides by a transverse wall into an upper and a lower cell; the former divides again by an oblique wall into an upper larger cell and a lower smaller one. The latter by several divisions gives origin to the stalk of the archegonium, and the former becomes divided by three vertical and oblique walls, into a central cell surrounded by a three-celled wall. By further divisions, the three-celled wall becomes converted into the venter and neck of the archegonium, and the central cell into the ventral and neck canal cells, and the ovum.

4. The Sporophyte or Sporogonium ('Fruit').

The first result of fertilization is the formation of a cell-wall round the ovum, which then elongates and divides by one or two transverse walls, i. e. at right angles to the long axis of the archegonium (Fig. 126, I). The uppermost and lowest of the two or three cells thus formed then divides by two oblique walls and thus forms in each an apical cell (Fig. 126, II, A & A') ; the upper apical cell in its turn cuts off two rows of segments ; each segment is then divided by a vertical wall, and also by numerous transverse ones. The oospore

has now become converted into a multicellular mass, oval in form, and lying within the enlarged venter of the archegonium ; this body is the young sporogonium, and it continues for some time to grow by means of its apical cell. The young sporogonium (sporophyte) continues to elongate, and for some time the archegonium keeps pace with it ; but ultimately, the sporogonium growing the faster of the two, the former is ruptured about the middle of the venter (Fig. 126, III), and the neck and upper part of the venter is carried upwards as a cap (C) covering the sporogonium ; this cap, called the **calyptra**, in some mosses early withers and disappears, but in others it is retained until the sporogonium is ripened; the lower portion of the venter (Fig. 126, III, V) forms a membranous investment, called the **vaginula** (Fig. 127, I, V), round the base of the sporophyte. The lower portion of the sporogonium now begins to elongate very rapidly, forming a stalk-like structure, called the **seta** (S), which grows downwards into the substance of the stem, to which it acquires a hooked attachment, but does not form any organic connexion. At the top of the seta, the sporogonium forms a swollen-like body, called the **theca** (T) or **capsule**, which is at first filled with an undifferentiated tissue : but soon differentiation of this tissue begins, and ultimately, in *Polytrichum* (Fig. 127, III) it forms a central column of parenchyma, the **columella** (C), and an outer investing wall, composed of an outermost layer of lignified cells (Fig. 127, III and V, E) with three layers of soft parenchyma (P); between the columella and the wall of the theca there is developed, at a stage earlier than that figured, a cylindrical wall of tissue called the **spore-sac**, separated from the columella in the centre and the wall of the capsule by an air-space on either side of it, which are traversed by filaments of thin-walled, elongated cells. The spore-sac is the essential portion of the whole structure, for from it the spores will be produced. It consists of several layers of

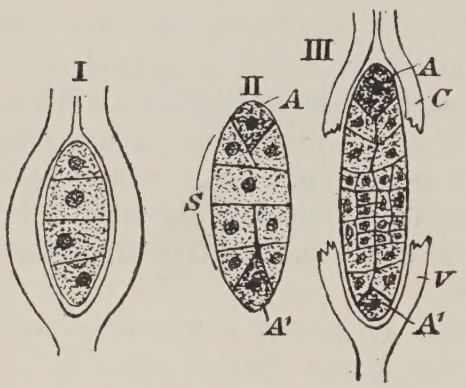


FIG. 126. Development of the sporophyte in *Polytrichum*. I. Segmentation of the oospore. II. Formation of two apical cells. The archegonial wall is not represented. III. Formation of the tissues of the sporophyte and bursting of the archegonial wall. Magnified 300 times. A and A'=upper and lower apical cells respectively; C = calyptra; S= developing sporogonium (sporophyte); V = vaginula.

parenchymatous cells, of which, however, a middle row becomes early conspicuous by the larger size of its cells, their denser protoplasm and larger nuclei; each cell in this layer is a **spore mother-cell** and by subsequent division into four forms four **spores**. When the spores are quite ripe, the parenchymatous layers of the spore-sac, as well as the filamentous layer, and in part also the tissue of the columella, break down, so that the spores (SP) are liberated into the air-space of the capsule (AS). Fig. 127, III, represents the capsule at this stage.

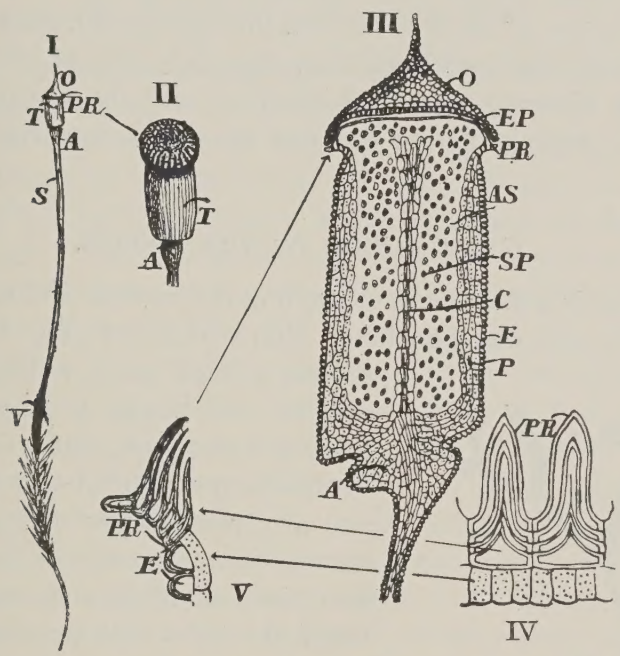


FIG. 127. **I.** A whole plant of *Polytrichum commune* with the 'fruit.' Natural size. II. The capsule of the 'fruit' enlarged two and a half times and viewed obliquely from above, after removal of the operculum. III. Median longitudinal section of a capsule. Magnified 300 times. IV. A portion of the peristome seen from the inner surface. Magnified 300 times. V. A portion of the peristome seen in longitudinal section. Magnified 300 times. A=apophysis; AS=air-space; C=columella; E=outer wall of capsule; EP=epiphragm; O=operculum; P=parenchyma of wall of capsule; PR=peristome; S=seta; SP=spores; T=theca or capsule; V=vaginula.

Meanwhile, however, the capsule has been undergoing remarkable changes at its upper part, producing certain structures instrumental in the dehiscence of the capsule and the dispersion of the spores. The capsule is closed above by a cap-like lid called the **operculum** (O), which when the capsule is mature very easily breaks away from it; if it be artificially removed, it will be found that the capsule is closed still, by a very thin membrane, called the **epiphragm** (EP). Upon removal of this, the mass of dust-like spores within the capsule

can be seen, and round the margin of the aperture is a thick, orange-coloured rim, bearing a number of teeth, which are bent slightly inwards; this is the **peristome** (Fig. 127, PR), and it is instrumental, in virtue of its hygroscopic nature, in dispersing the spores, since in wet weather the teeth of the peristome bend inwards and tend to keep the spores within the capsule, and in dry weather bend suddenly upwards and outwards, carrying some of the spores with them. Each tooth of the peristome consists of several elongated, pointed, thick-walled cells (Fig. 127, IV and V) fused together.

At the junction of the seta (S) with the capsule (T), there is a marked swelling called the **apophysis** (A), the epidermis of which in some mosses, e. g. *Funaria*, possesses stomata, and the greater portion of the internal parenchymatous tissue of which is laden with chlorophyll grains.

GERMINATION OF THE SPORES.

Each spore is a single cell containing chlorophyll and oil drops, and covered with two walls, an inner, thin endospore (Fig. 128, EN), and an outer, thick exospore (EX). In damp soil, the cell begins to grow and bursts the outer exospore, when the endospore begins to protrude at two points. The two protrusions grow out and form filaments, of which one (F) becomes green and creeps along the surface of the ground, while the other (R) penetrates the soil, remains colourless, and forms the first rhizoid. Both filaments increase at first by the formation of transverse septa, but very quickly an apical cell is formed in both cases; these cut off successive segments arranged in a single row, so that the filaments remain as such throughout their existence. The filaments branch very profusely (Fig. 128), each branch arising as an outgrowth just behind a transverse septum. The filamentous structure which thus arises is called a **protonema**, and it is a very characteristic feature in the life-history of mosses; by whatever means a new moss-plant may arise, with but an isolated exception, its early stage is always that of a protonema.

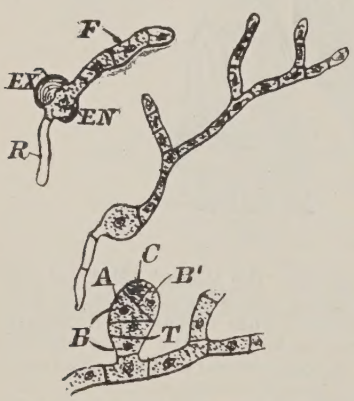


FIG. 128. Germination of the spore and formation of the protonema of a moss. A = acroscopic side; B = bud; B′ = basiscopic side; C = apical cell; F = protonemal filament; R = rhizoid; T = a transverse wall of bud.

Upon the protonema many moss-plants may arise. Each one first takes its origin as a small outgrowth (Fig. 128, lowest figure, B), which first divides by one or two transverse walls (T), and then by an oblique wall, dividing the bud into an acroscopic (A) and basiscopic (B′) side. An oblique septum is then formed in the basiscopic portion, thus cutting off an apical cell (C) at the apex of the bud. From this apical cell, segments are regularly cut off, and a new moss-plant arises.

5. Vegetative Reproduction.

In addition to the asexual reproduction of a protonema from spores, the moss-plant can vegetatively reproduce by several methods. If some leaves of *Funaria* be cut off and placed on damp soil under a bell-jar for about a week, protonemal filaments will grow out from them and may produce new moss-plants in the same way as those derived from spores do. These filaments arise by the vegetative growth of a single cell of the plant. They may arise from any part of the moss-plant : from a single cell of the leaf or stem, or the rhizoids, and even from the capsule. They may be readily produced from the rhizoids of *Funaria* by simply inverting a sod of the moss, so that the rhizoids are exposed to light, and placing them under a bell-jar in order to secure a moist and warm atmosphere. Some mosses produce protonemal filaments at the apex of the stem, and these develop cellular bodies of a lenticular form at their free extremity, called **gemmæ**. These are detached from the parent plant, and while on the ground produce, by the outgrowth of one of their marginal cells, a protonemal filament, which gives rise to a flat, pear-shaped body, the **pro-embryo**. From the base of this, a leaf-bud may grow out and form a new moss-plant.

The root-hairs (rhizoids) may give rise to a leaf-bud directly without the intervention of a protonema : these may arise either on the aërial rhizoids or on those which have penetrated the soil ; in the former case, they grow at once into a moss-plant, but in the latter they remain dormant, form a reserve store of food-material, and wait until they chance to reach the surface of the ground.

Comparing the life-history of the moss with that of the fern, we find that in both there is a distinct alternation of generations, though there is a transposition of parts, inasmuch as the leafy shoot in one case belongs to the sporophyte generation, and in the other to the gametophyte. But there is a further difference, for in the fern the two genera-

tions are independent, and each capable of existing without the other ; while in the moss, the sporophyte generation is reduced to a mere appendage upon the gametophyte, depending in very large measure upon it for its food supply. There are, however, degrees of dependence of the sporophyte upon the gametophyte among mosses, for in *Funaria* and others a great portion of the parenchyma of the capsule, especially that in the apophysis, contains chlorophyll, and the superficial layer of the capsule has numerous stomata, so that it can perform a certain amount of CO_2 assimilation on its own account. And it has been experimentally shown in certain cases that the capsule can grow and live when separated from the gametophyte. But none the less, when a general survey of the mosses is made, it is obvious that there is an intimate physiological connexion between the two generations. And when we take into consideration the fact that indubitable prothallia (gametophytes) may arise directly from the leaf of the fern, and vice versa, we begin to ask whether the doctrine of the 'alternation of generations' can any longer be regarded as an expression of fact. Are not the phenomena which are exhibited more correctly interpreted by regarding each so-called generation as being merely different stages in a process of development? This occasional intimate relationship between the two generations, under certain circumstances, has been already alluded to when describing apospory and apogamy in the fern, and we have further seen that in the moss the gametophyte, as represented by a protonema, may arise directly from the wall of the capsule (sporophyte generation). Hence, neither in the fern nor the moss are the two generations distinct, in the sense that the one is never more or less merged with the other, so that no break in the organic continuity exists, where it is possible to say the one begins and the other ends.

The great development of the protonema and its almost constant occurrence in all forms of reproduction is a very characteristic feature among mosses, and contrasts strongly with its weak development among ferns ; in some of the latter, however, the prothallium exists as a protonema up to the time when sexual organs are formed, when it widens into a plate-like structure. But it never reaches in ferns the same degree of development, nor plays such a conspicuous part in the life-history, as in mosses ; in fact, it does not do so in any other group of plants.

The constant occurrence of an apical cell in the development and growth of *every* organ again marks off the true mosses from the ferns.

In both mosses and ferns the sexual organs are built upon the same plan, but in mosses the neck of the archegonium is very long, and the venter is composed of two layers of cells.

On the whole, and especially in virtue of the leafy shoot-like gametophyte and the conspicuous part played by the protonema, mosses are an isolated group of plants.

CHAPTER XIII

THE LIVERWORTS (*Pellia epiphylla*)

Gametophyte Generation.

1. Structure of the Thallus.

Like the mosses, liverworts have a very distinct alternation of generations, and the gametophyte is the more obvious and important of the two; the sporophyte is an appendage of the gametophyte, and its structure is very simple. The gametophyte not only produces reproductive organs, but it performs the vegetative activities of life as well, whereas the sporophyte does nothing more than develop the asexual reproductive spores, and depends upon the gametophyte for its nourishment.

Pellia is among the commonest of liverworts, and may be found almost everywhere; in damp gullies, on the banks of streams, at times actually under water, in forests, copses, and in hedgerows; not infrequently it may be found on the surfaces of sandy rocks, and it is plentiful on the surfaces of pots in neglected greenhouses. Usually it is to be found in tangled masses often of great extent.

Examination of one of the individual plants (Fig. 129) shows it to be composed of a branching plate of green vegetable tissue, in which there is no differentiation into stem, leaf, or root. Such a plant is called a **thallus**, and the student will recall the fact that the prothallium of the fern is of this nature. In fact, the vegetative structure of the thallus is very similar in both cases, the chief difference being that in *Pellia* it branches, whereas in most ferns it is unbranched. The branching is dichotomous and in one plane, so that the thallus has obvious upper and under surfaces. On the under surface

numerous unicellular rhizoids arise (Fig. 132, R), by means of which the thallus is attached to the substratum and mineral matter in solution in water is taken up. The thallus is traversed by a midrib, formed by a simple thickening of the tissue, and on either side of this it thins away towards the margin.

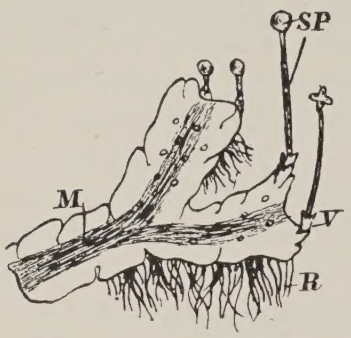


FIG. 129. A whole plant of *Pellia* seen from the upper surface, at the 'fruiting' stage. M=midrib; R=rhizoids; SP=sporophyte; V=calyptra. The sporophyte to the right has dehisced or opened. Natural size.

The form of the thallus varies according to the conditions under which it lives; in dry situations it is stumpy and thicker, with the midrib not well marked, but in an aquatic environment it is elongated and thin, with a very pronounced midrib. Under its most favourable conditions, as in damp positions, the thallus is long, with pronounced midrib, but broader than in the wholly aquatic form.

The structure of the thallus is very simple, for it consists wholly of parenchyma (Fig. 135); the cells of the midrib are elongated, but elsewhere polygonal in form. The epidermal cells (E) are slightly flatter than the rest, but otherwise do not differ from them; stomata are not present in *Pellia*, but in other liverworts, such as *Marchantia*, specialized stomata are developed. All the cells contain chlorophyll plastids and starch grains embedded in them, but these are more numerous in the upper superficial layers than elsewhere.

The front end of each thallus is distinguished by a depression; at the bottom of this is the growing point, which is made up of a single large apical cell, which cuts off segments in three planes, i. e. from either side and from the base. The former segments divide and contribute to the formation of the lateral parts of the thallus, while the midrib is formed by the tissue derived from the basal segments.

When a thallus branches it does so by the division of the apex into two equal branches, each of which grows equally vigorously. The two apical branches are formed by one of the lateral segments cut off from the parent apical cell, becoming converted into another apical cell; both cells go on growing and dividing on their own account, and so the two branches are formed.

2. The Sexual Organs.

(*a.*) The Antheridia or Male Organs.

The antheridia (Fig. 130) are borne in pocket-like depressions on the upper surface of the thallus. Each one consists of a spherical case, with a single-layered wall, and encloses a mass of very small cells, which are the mother-cells (SP) of the spermatozoids. The spermatozoids (S) arise from the nucleus of the mother-cells by the elongation and twisting of the nucleus, while the two cilia are derived from the protoplasm of the cell. The pocket-like depressions in which the antheridia are borne, one in each pocket, open to the

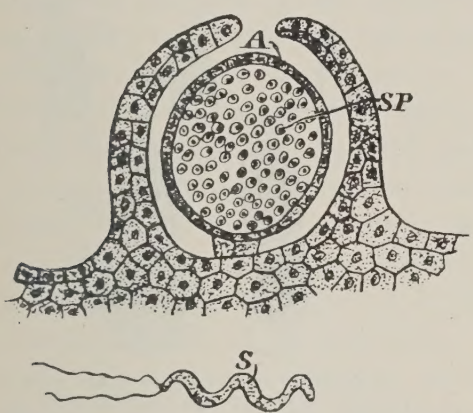


FIG. 130. Section through the upper surface of a thallus passing through a 'pocket' and an antheridium of *Pellia*. Magnified 270 times. A=wall of antheridium; S=spermatozoid; SP=spermatozoid mother-cells.

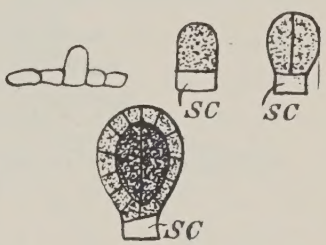


FIG. 131. Development of antheridium of *Pellia*. SC=stalk-cell. The left-hand figure represents a few epidermal cells with one of them growing outwards, and from the further development of which the antheridium will arise.

exterior by a small aperture only, and the sheath which closes over the antheridium and forms the upper part of the pocket in which it lies, arises as an upgrowth of the tissue of the thallus.

Each antheridium arises from a single superficial cell, not far behind the growing point. This cell bulges out, and then divides by a transverse wall into an upper and a lower cell (Fig. 131). The lower cell divides once or twice, and forms the stalk. The upper cell elongates slightly, and then divides by a vertical wall (Fig. 131); two walls parallel to the surface of each of the two cells are then formed, dividing each into an outer and an inner part. The outer part divides up by the formation of anticlinal walls (at right angles to the surface), and gives rise to the wall of the antheridium, while the inner portion divides up repeatedly, and gives rise to the

spermatozoid mother-cells. While these changes are going on, the tissue of the thallus round the developing antheridium grows up around it and encloses it, leaving a small aperture, however, at the top; thus is formed the pocket in which the antheridium lies.

(*b.*) The Archegonia or Female Organs.

The archegonia (Fig. 132, AR) are identical in structure with those of mosses, consisting of a long neck, of a venter, which is at first single-layered but becomes two-layered after fertilization, of an ovum, of a ventral-canal cell, and of several neck-canal cells. They are situated

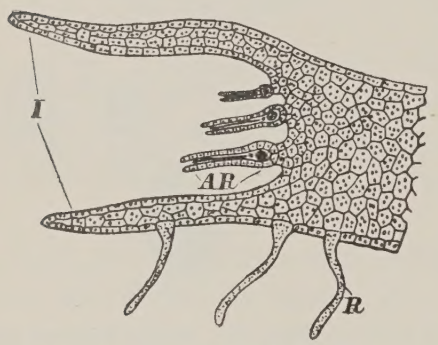


FIG. 132. Longitudinal section through front part of thallus of *Pellia*. AR = archegonium; I = involucre; R = rhizoid. Magnified 270 times.

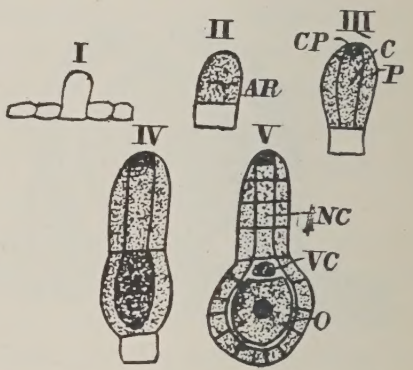


FIG. 133. Development of the archegonium of *Pellia*. AR = upper cell from which the archegonium is developed; C = central cell from which the neck-canal cells, ventral-canal cell, ovum, and cap-cell are derived; CP = cap-cell; NC = neck-canal cells; O = ovum; P = peripheral cells from which the wall of the archegonium is derived; VC = ventral-canal cell.

at the end of the thallus, and lie in pocket-like depressions called the involucres (Fig. 132, I). In dry situations the involucre is characterized by its long flaps, while in aquatic positions it is very short; the involucre protects the essential female organs from mechanical injury, and prevents their rapidly drying on hot dry days by the moisture which is retained in its more or less closed cavity.

Like the archegonia of the fern, those of the liverwort arise from a single superficial cell of the thallus. This cell is situated just behind the growing point, and it bulges out beyond the surface of the thallus as a small papilla (Fig. 133, I). It then divides by a transverse wall (Fig. 133, II) into an upper and a lower cell;

from the latter the stalk is formed, and from the former the archegonium itself. The upper elongates, and then divides by three vertical walls (Fig. 133, III), so that three peripheral cells (P) and a central one (C) are formed; a little later, the peripheral cells divide again by vertical walls, so that their number becomes increased to five or six, and from the top extremity of the central cell a small cap-cell (CP) is cut off. The whole mass of vertical cells is then divided into an upper and lower part by a transverse wall (IV); the former forms the neck and neck-canal cells of the archegonium, and the latter, the venter, ventral-canal cell, and ovum. The peripheral cells of the lower part divide up by anticlinal walls, and grow and constitute the wall of the venter, while the central cell divides into an upper very small cell, the ventral-canal cell, and a larger lower one, that becomes the ovum (O). The cells of the upper part, both peripheral and central ones, divide by numerous transverse walls, to form the neck and neck-canal cells (V). The cap-cell then divides by two vertical walls crossing each other at right angles, and forms a marginal lip at the extremity of the neck.

If we compare the archegonium of a liverwort with that of a fern, we see that it differs from it in the great length of its neck, and in the origin of the neck-canal cells. In ferns the neck-canal cell arises as an outgrowth of the ovum, which becomes constricted off from it, but in liverworts, as we have seen, it is derived from the upper part of the archegonium. And the same contrast is true when we make it with *Selaginella* or any other vascular cryptogam. But apart from these detailed differences, the fundamental nature of the archegonium is the same in mosses and liverworts and the vascular cryptogams.

When ready for fertilization, the neck-canal cells and the ventral-canal cell break down into a mucilaginous slime, which by the absorption of water swells, and bursts open the four cap-cells at the end of the neck, thus allowing the mucilage to exude beyond the lip, and placing the ovum in communication, through the canal of the neck, with the exterior.

Fertilization in *Pellia* is identical with the same process in mosses and vascular cryptogams. The spermatozoids when ripe are liberated by the rupture of the antheridial wall into the thin film of moisture that invests the thallus, and swim about until they come near to an archegonium. When they reach within a certain distance of it (sphere of influence), they turn aside and swim directly towards the orifice of the neck. The mucilaginous slime in *Pellia*, as in the other cases we

have considered, thus exercises a directive influence on the spermatozoids, but the nature of the substance which exercises this influence is not yet determined. The spermatozoids wriggle down the neck of the archegonium, and one of them penetrating the ovum finally reaches its nucleus, with which it fuses. The ovum then surrounds itself with a cell-wall, and begins to divide. The embryo which results is very similar to that of the moss, and is essentially a spore-bearing capsule, in which the vegetative functions have disappeared, the organism being alone concerned with the production of spores.

3. The Sporophyte or 'Fruit.'

The fertilized ovum divides into two by a transverse wall (Fig. 134, I). The lower cell takes no further part in the development of the embryo. The upper cell divides by a vertical wall (II) into two; then each of these is divided into an upper and a lower cell by a transverse wall (III). The upper two cells by further divisions form the capsule or spore-bearing case, the lower gives rise to the stalk or seta. Thus at this early stage, the parts of the sporophyte are already marked out. The whole of the four cells then become divided by periclinal walls (parallel to the surface) into a peripheral and a central part (IV). The central portion of the upper set of cells (those that form the capsule) is the **archesporium**, and by repeated divisions this gives rise to the **spore mother-cells**. The other cells divide up repeatedly, and the young sporophyte becomes an elongated embryo of the form shown in Fig. 135, S. At the front end is the archesporium (A), and behind this the tissue of the developing seta. At this stage the sporophyte is invested by a single layer of cells, but later this becomes two or three layers thick. The whole is enclosed in the enlarged venter of the archegonium, the wall of which becomes several layers thick. As the sporophyte grows, the archegonium and also the tissue of the thallus at its base grow also, and keep pace with it, for a time. There are thus carried

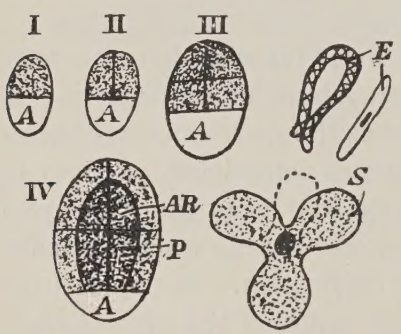


FIG. 134. Development of the sporophyte in *Pellia*. I. First segmentation of oospore. II. Second segmentation. III. Third segmentation. IV. Later stage. A = lower cell; AR = archesporium; E = elaters; P = peripheral cells from which wall of sporophyte is derived; S = spore mother-cell.

up with the calyptra several abortive (unfertilized) archegonia (AB). After a time the calyptra is ruptured by the growing sporophyte, and it then remains as a withered investment at the base of the latter. During these changes, the seta has been growing into the tissue of the thallus, where it forms a conical and barbed foot, so that it is held in the tissues of the gametophyte, very much in the same way that it is in the moss. There is, however, no continuity of tissue ; structurally the connexion is merely a mechanical one, though physiologically it is more intimate, and the sporophyte is nourished by nutriment provided by the gametophyte.

The archesporium has at this stage divided up a great many times and formed the spore mother-cells, and in addition a large number of elongated cells, called **elaters**, which are instrumental in the disper-

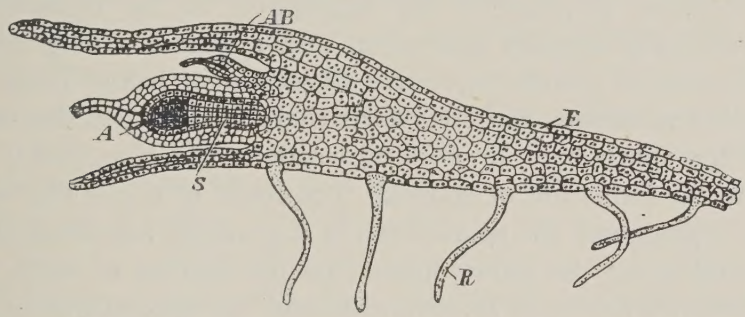


FIG. 135. Longitudinal section through the thallus of *Pellia*. A=archesporium; AB= aborted archegonium; E=epidermal layer; R=rhizoids; S=developing sporophyte. The letter points to the part of the sporophyte that will later become the seta. Magnified 270 times.

sion of the spores. The spore mother-cells (Fig. 134, S) are of a peculiar form. At first they are spherical, but subsequently each grows out into four blunt processes, the nucleus of the cell remaining at the centre. In a short while, the nucleus divides into four, and one nucleus passes into each of the processes, which then become constricted off from each other, and form four **spores**. The elaters become more elongated and bend upon themselves, lose their protoplasm, and become spirally thickened, by the formation of a very thin spiral band of a corky nature.

By this time, the seta has elongated enormously, and the capsule becomes carried upwards, and presents the appearance depicted in Fig. 129, SP. The sporophyte is now ripe, and dehiscence takes place by the formation of four longitudinal splits, so that the capsule opens by four valves. If the weather be dry, the corky elaters suddenly bend straight and jerk the spores out in all directions.

The spores of *Pellia* are exceptional among liverworts in that their germination commences while still enclosed within the capsule. If we examine some spores from a ripe capsule, we shall see that they are not unicellular bodies, but composed of several cells containing chlorophyll, so that each one contains a very young thallus. From one of the terminal cells an apical cell is cut off, and this continues the growth of the thallus, when the spores are shed on to damp earth. Other cells grow out and form the first root-hairs.

The life-history of *Pellia* is thus very similar to that of the moss. In both, the gametophyte is the more important generation, while the sporophyte is reduced to a spore-bearing sac. The sexual generation of the liverworts and mosses is obviously comparable to the gametophyte of the fern and *Selaginella*, but the sporophyte is very different. In the vascular cryptogams the sporophyte is the important and more structurally complex generation, and it passes a long and complicated course of purely vegetative development before it forms the spores ; but in mosses and liverworts there is no vegetative development of the sporophyte, or nothing worth considering, and it passes at once to the formation of spores. The result of this is that while in vascular cryptogams the sporophyte is a perfectly independent plant, not dependent on the gametophyte for its sources of food, in the mosses and liverworts it is otherwise, and the sporophyte to a very great extent, and in some cases wholly, is dependent upon the gametophyte for its nutriment. The respective importance of the two generations is thus reversed.

CHAPTER XIV

(C.) THALLOPHYTA

(*a.*) THE ALGÆ.

THE algæ are a group of plants, of which popularly the best-known representatives are the sea-weeds ; all sea-weeds in fact belong to the algæ. The majority of the plants belonging to this group are aquatic, some inhabitants of fresh water, others of the sea ; many, however, live on the damp surfaces of the soil. They comprise among them some of the simplest forms of living things that are microscopic in size, and also forms of relatively complex structure and great size. Their methods of reproduction and their habits are very various, and the

different families differ from one another more than the ferns differ from the phanerogams.

Unfortunately the types of algæ which we have to study are quite insignificant in number, and can afford no adequate idea of the variety, and the many different lines of structural divergence which the group presents.

(*a.*) PHÆOPHYCEÆ (BROWN ALGÆ).

FUCUS SERRATUS (*Wrack*).

1. External Characters.

Fucus is a sea-weed of very general occurrence along our coasts, and is to be found, usually in great quantities, at about mid-tide level. It is a branched thallus (Fig. 136), of dark olive colour, with serrated margins, truncated and depressed apices, and attached to the rocks by an expanded disc-like organ, called the **disc**. Examination of any portion of the thallus reveals the presence of a central, thickened ridge, the midrib (M), which if it be traced backwards will be found to increase in thickness, and ultimately at the basal portion of the plant is the only part of the thallus that remains, the lateral expanded margins having disappeared; this basal portion of the thickened midrib is the so-called '**stalk.**'

The branching of the thallus is that of a true dichotomy, i. e. the two branches are formed at the apex and develop equally, so that the thallus is composed of a number of two-pronged fork-like branches; although the origin of the branches is that of a true dichotomy, nevertheless it will be found that one of each pair of branches develops slightly more strongly than the other, so that a sympodial development of the dichotomy results.

Examination of the surface of the thallus reveals a number of minute dot-like elevations (Fig. 136), scattered here and there, and on the summit of each is an aperture. These are hemispherical chambers called **sterile conceptacles** (S.C), containing a number of hairs, some of which project from the aperture or **ostiole**, and form a tuft just large enough to be seen with the unaided eye.

At the upper portion of certain of the branches, a large number of dot-like swellings will be found crowded together, and the portion of the thallus upon which they are situated is slightly thicker than the other parts, and is distinguished as the **receptacle** (R); these dot-

like swellings mark the position of the **fertile conceptacles** (F.C), and in the winter months hairs project from them, which are orange coloured in the male and olive-green in the female conceptacles. There are several species of *Fucus*, and in *F. serratus* and *F. vesiculosus* the male conceptacles are borne upon one plant and the female upon another, while in *F. platycarpus* both male and female elements are found in the same conceptacles.

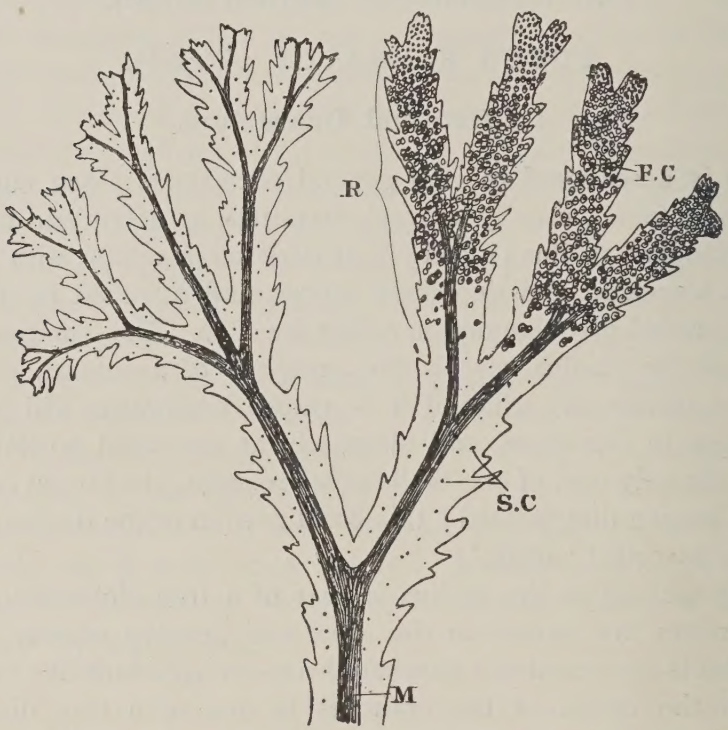


FIG. 136. The terminal portion of the thallus of the Wrack (*Fucus serratus*), showing a reproductive (on the right) and a vegetative branch (on the left). One-third natural size. F.C=fertile conceptacles; M=midrib; R=receptacle; S.C=sterile conceptacles.

The colouring matter which gives to *Fucus* its olive colour is a compound material, composed of a yellow substance, phycoxanthine, a green one, chlorophyll, and a reddish-brown one, phycophæine. The green substance is contained in the chlorophyll grains, the reddish-brown substance appears to adhere to them, and the yellow substance is dissolved in the cell-sap. The phycoxanthine and phycophæine are soluble in fresh but not in salt water, and the chlorophyll is soluble in neither, so that the green colour of the plant is easily demonstrated by placing the thallus in fresh water.

2. Internal Structure.

The thallus is limited externally by a layer of radially elongated cells (Fig. 137, L), which have thick and cuticularized outer walls, but thin radial and tangential ones. Careful observation of good preparations shows that this outer layer of cells is an actively dividing one, since the cells are of neither uniform depth nor width, and some of the radial (anticlinal) and tangential (periclinal) walls are thinner than others. The want of uniformity in the size of the cells, and the thinness of some of the walls, is an indication of the formation of new cell-walls, of which the latest formed cells are the smallest, and their walls the

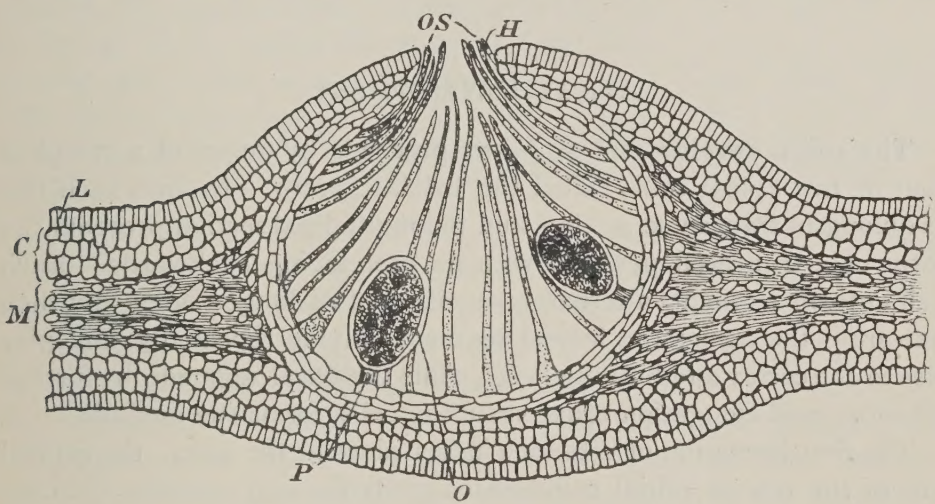


FIG. 137. Transverse section through a portion of the reproductive part of the thallus (receptacle) passing through a female conceptacle of *Fucus serratus*. Magnified 300 times. C=cortex; H=hairs; L=limiting layer; M=medulla; O=oogonium; OS=ostiole; P=pedicel of oogonium.

thinnest. This layer cannot, therefore, be called an epidermis, and it is perhaps best distinguished by the term **limiting layer**. Within it is a **cortical band** of cells (C) approximately square in outline, with thick cellulose, simply-pitted walls, and containing protoplasm and chlorophyll grains; in longitudinal sections the cells are somewhat elongated, and the transverse walls are thinner than the others. Centrally the thallus is occupied by a soft **medulla** (M), composed of elongated filaments (**trabecular tissue**), the outer layers of the cell-walls of which are mucilaginous and swollen, while the innermost layer retains its cellulose character; the transverse septa are very thin and are perforated by apertures like sieve-plates: it is possible, therefore, that the medulla is a conducting tissue.

The 'stalk' or basal part of the thallus is devoid of a limiting layer and is composed wholly of cortical parenchyma and medulla; the limiting layer in the older parts of the thallus over the midrib is a quiescent tissue, while the cells of the cortical parenchyma are still actively dividing, the result of which is that the outer layer is ultimately thrown off. The activity of the cortical tissue not only increases its own bulk, but it also adds new filaments to the central medulla. An examination of a series of sections, made through successively older parts of the thallus, will thus show that the midrib arises as the result of the increase of the cortical parenchyma and medulla, the latter to a greater extent than the former.

Apical Development.

The apical development of *Fucus* proceeds by means of a *group* of four or five apical cells, called the **initial group.** In form each cell is oblong in transverse section, and in longitudinal section presents the form of a truncated pyramid with its base facing backwards. Each cell cuts off segments alternately on either of its longer sides, and then one from the base: the lateral segments divide repeatedly, and give rise to the cortex and limiting layer, while the basal segment, by further divisions and elongation of the resulting cells, forms the medulla.

The first formation of a branch takes place at the apex; the central one of the row of initial cells ceases to divide and assumes the condition of permanent tissue, thus dividing the single group into two, each with two initial cells. The initial cells then divide into two equal parts, and one of these may divide again, thus bringing each group up to the original number of cells; from each group a new branch arises.

3. Organs of Reproduction.

Reproduction in *Fucus* is wholly by the sexual method, though in some Fucaceæ, e.g. *Pelvetia*, new branches may arise by purely vegetative growth, to replace those torn off by the violence of the waves.

The reproductive organs (Fig. 137) are contained in hemispherical cavities, called **conceptacles,** each of which opens to the external water by a minute aperture, the **ostiole** (OS). The conceptacles are lined by a small-celled tissue, from which numerous hairs (H) proceed,

that almost fill the cavity of the conceptacle, while some of them project through the ostiole. Some of these hairs, in the male conceptacles, do not branch; others, however, bear lateral branches, and upon the ends of some of these, little oval bodies, the antheridia, are borne. Each **antheridium** (Fig. 138) consists of a single cell, the wall of which becomes divided into two layers, an outer, firmer **extine** (E), and an inner, mucilaginous **intine** (I); the protoplasm of the cell becomes divided into a large number of little masses, the spermatozoid mother-cells (S), the nuclei of which ultimately elongate into little pear-shaped bodies, each of which possesses two cilia borne laterally, and acquire an orange-coloured globule; these are the **antherozoids** or **spermatozoids**.

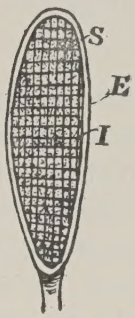


FIG. 138. Antheridium of *Fucus serratus*. Magnified 300 times. E=extine; I=intine; S = spermatozoid mother-cells.

The **oogonia** or female organs, like the antheridia, are metamorphosed hairs, and each one arises as a little papilla-like projection of one of the lining cells of the conceptacle, which divides by a wall into an upper and a lower cell; the latter forms a unicellular stalk or pedicel (Fig. 137, P), while the former enlarges into an oval body (O), the protoplasm of which becomes divided into eight portions, the **oospheres**, while the wall splits into two layers, an outer **extine** and an inner mucilaginous **intine**. The protoplasm of the oospheres is very granular and each one contains a single nucleus.

When ripe, both oogonia and antheridia are liberated from the conceptacles by the bursting of the extine; and the intine swelling by imbibition of water, allows of the escape of the oospheres and spermatozoids. The latter crowd round the former, and so energetic are their movements that they impart to it a rotatory motion: ultimately one of the spermatozoids penetrates the protoplasm of the oosphere and fuses with its nucleus.

DEVELOPMENT OF THE OOSPORE.

The first result of fertilization is the formation of a cell-wall round the oospore. There is no period of rest, and within a few hours after fertilization the oospore divides into two; further divisions take place, and the young plant begins to elongate, at the same time putting forth root-like prolongations of those cells farthest removed from the source of light. These attach the young plant to the substratum on which

it is resting. A depression next appears at the summit, and beneath this an apical cell is formed, from which new tissues arise as in the mature plant.

(4) The Life-History.

There is no 'alternation of generations' in *Fucus*, the whole life-history consisting only in the existence of the gametophyte or sexual plant: the oospore does not give rise to an asexual spore-bearing plant, but directly to the sexual organ-bearing one. In a sense, therefore, the Fucus-plant is comparable to the moss-plant or the prothallium of the fern, but it differs from them in the structure of the sexual organs, for the archegonium, so characteristic of all the higher plants from the liverworts upwards, is absent here. In *Fucus* the sexual organs are very simple—almost reduced to the simplest condition consistent with the sexual method of reproduction; and in some *Fucaceæ* (*Cystoxira*, *Halidrys*, and *Himanthalia*) the female organ is more simple than that in *Fucus*, inasmuch as its protoplasm remains undivided, and forms therefore but a single oosphere.

The structure of the vegetative portion of the plant is comparatively somewhat complex, and is specialized along structural paths adapted to its habits, as is evidenced by the permanent retention of the merismatic characters of its tissues, by means of which injured surfaces may be repaired after damage inflicted by the buffeting of the waves.

(β.) The Chlorophyceæ (Green Algæ).

The *Chlorophyceæ* is a family of algæ which includes the great majority of the fresh-water representatives of the group, and some few of the marine forms. They are mostly exceedingly simple in their vegetative structure, and are either unicellular, filamentous, or a flattened plate as in *Ulva*. We shall study four members of the family, i.e. *Ulothrix*, *Vaucheria*, *Spirogyra*, and *Protococcus*.

ULOTHRIX ZONATA.

(A.) Structure of the Thallus.

The period of activity of this alga is winter, not summer, and it may be found in early spring in slowly-flowing streams and ponds, and in cattle-troughs. Each individual plant is a filament of exceedingly small size, measuring about the one-thousandth of an inch in diameter, and is either attached by one end to the substratum, or floats free in

tangled masses. Each filament is unbranched, and consists of numerous cells arranged end to end in a single series (Fig. 139, I). Each cell is square, or but slightly elongated, with a cellulose cell-wall, enclosing a thin film of protoplasm, in which is embedded a single nucleus. Lying immediately within the cell-wall in the pellicle of protoplasm is a cylindrical chloroplastid, often as long as the cell itself, but usually slightly shorter. The specific name of the plant is due to the zone-like form of the chloroplastid. The central part of the cell is filled with cell-sap. The whole filament grows in length, and its cells divide as growth proceeds; there is no special growing point.

(B.) Modes of Reproduction.

Ulothrix reproduces by means of active spores, called **zoospores.** Of these there are two kinds, distinguished by the number of their cilia. One form possesses two cilia, and the other form four cilia, and are known respectively as the **biciliate** and **quadriciliate zoospores.** As a rule the spores of the latter form are slightly larger than those of the former, though there is considerable variation in the size of either form. The spores may arise from any of the cells of the filaments by the simple division of its nucleus (Fig. 139, I, 1), followed by that of its protoplasm.

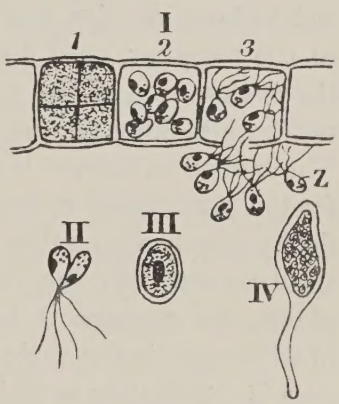


Fig. 139. *Ulothrix zonata.* I. Three stages in the formation of zoospores. II. Two biciliate zoospores conjugating. III. A resting zygospore. IV. A germinating zygospore. (Based on Dodel-Port.)

The quadriciliate zoospores (I, z) are produced to the number of either two, four, or eight from a single cell, according to its bulk or size. Each zoospore is pear-shaped, with four cilia attached at its narrow end, and by the rapid vibrations of which the zoospore is propelled through the water. Each one possesses a contractile vacuole, a red-coloured spot, and a chloroplastid situated at the broad end of the spore. The quadriciliate zoospores are asexual bodies and swim about very actively for some time, but ultimately come to rest; they lose their cilia, become attached to the substratum by their narrow and colourless end, and, surrounding themselves with a cell-wall, grow into a new *Ulothrix* filament by the simple process of growth in length and transverse cell-division.

The zoospores are sensitive to light, avoiding very bright light, but seeking diffuse light. In darkness they become uniformly dispersed through the water and never rest. Under ordinary conditions, sooner or later, they endeavour to avoid the light altogether, and come to rest in dark situations, when they begin to germinate. Light exercises a retarding influence on growth, so that when the zoospores come to rest in deep shade, the conditions are favourable for their rapid growth.

The biciliate zoospores (II), like the quadriciliate ones, are formed from any of the cells of the filament, but they are formed in greater numbers, eight, sixteen, thirty-two, or even more in each cell. As their name implies, they possess only two cilia. Otherwise, they are like the quadriciliate forms, except that, as a rule, they are slightly smaller. They are liberated from the parent-cell in swarms, and at first swim about in swarms. When the zoospores of one swarm meet those of another, they become entangled by their cilia (II). They then swim about in pairs, and gradually the protoplasm of their cells begins to run together, until finally the two cells are wholly merged. After the coalescence of the two cells, they retract their cilia and come to rest by attaching themselves at their colourless end to the substratum. The body thus formed is called a **zygospore** (III). It is a body formed for the purposes of reproduction, but instead of arising as other spores do by purely vegetative processes, it is formed by the fusion of two similar cells. We saw that in the mosses and liverworts, and in higher plants, the oospore is formed by the fusion of two dissimilar cells, of which one is the male and the other the female cell. Such a process is a definitely sexual one, but in *Ulothrix* it is not possible to say which of the two coalescing cells is male or female, so that we cannot regard the formation of a zygospore as a distinctly sexual process. It is therefore necessary to be able to distinguish it from the undoubted sexual process by some distinctive term, and we speak of it as **conjugation.**

As a rule, a zygospore is a resting spore; that is, it undergoes a shorter or longer period of quiescence before it germinates. It then gives rise directly to a new plant. But in *Ulothrix*, although the zygospore undergoes a period of rest, it does not, as in other instances, give rise to a new plant at once, but grows into a unicellular plantlet (Fig. 139, IV), with a little colourless rhizoid at one end which penetrates the substratum and attaches it. The plantlet then remains dormant until the approach of winter, when its protoplasm breaks up into a number of zoospores of the quadriciliate form. These then

swim about and probably reproduce the *Ulothrix* plant in the same way that the quadriciliate zoospores derived from the cells of the *Ulothrix* filament do; but this has not yet been observed.

So long as the external conditions are favourable, *Ulothrix* reproduces in either of the two ways we have described. *Ulothrix* is exceptional in that its period of greatest growth is not summer but winter. During the cold months of the year, growth goes on rapidly, and reproduction is by means of the asexual quadriciliate zoospores, but as summer approaches, growth becomes sluggish and then zygospores are produced. They remain dormant until winter, when they germinate in the manner already described. This is the normal mode of reproduction so long as conditions are favourable, but should the water of the stream or pond in which the plant is living dry up, it resorts to another mode. The protoplasm of the cells divides up in all directions and forms colonies of rounded cells which repeatedly divide; finally, these rounded cells grow into *Ulothrix* filaments. This condition is called the *Palmella* condition, because the cells were originally mistaken for a distinct genus of algæ, to which this name was applied. In some instances the cells become surrounded by thick cell-walls, and undergo a period of rest until favourable conditions return.

Ulothrix is of special interest, because we find sexual reproduction manifested in its earliest beginnings. The conjugating zoospores are, as we have seen, very similar to the asexual ones, differing from them in the number of their cilia. The process of conjugation is sexual in as far as it involves the union of two reproductive cells, but it is not definitely sexual inasmuch as there is no differentiation into male and female cells. Thus we may regard conjugation as indicating the first step by which the sexual process arose from the asexual process, and that this is a reasonable interpretation is made more manifest when we learn the fact, that should the biciliate zoospores fail to conjugate, they can reproduce the plant asexually like the quadriciliate zoospores. The filament which thus arises is a dwarf one, but it is nevertheless a *Ulothrix* filament, so that while the biciliate zoospores have become sexual cells, they have not yet lost the asexual function and retain it as a vestigial character, capable of becoming active under special conditions.

We saw when studying the liverwort and moss that there is a definite alternation of a gametophyte with a sporophyte generation; that the former not only forms the sexual cells, but possesses a vege-

tative organization by means of which it is capable of obtaining food material and assimilating it, and so leading an independent existence, while the latter generation is reduced to a spore-bearing sac, so that its function is wholly confined to that of asexual reproduction. Now, in *Ulothrix* we have a kind of foreshadowing of this definite alternation of generations, in which the *Ulothrix* filament, as the generation that produces the conjugating zoospores, is comparable to the moss-plant or the liverwort thallus, and the unicellular plantlet derived from the zygospore, and which is merely a sac producing active spores, is comparable to the capsule or sporophyte generation of the moss or liverwort.

Thus in *Ulothrix* we see the advent of a sexual process of reproduction, and an indication of a gametophyte generation which has not yet lost the asexual process, and indeed in which the asexual mode of reproduction is still the predominant one. We see too the early stages, in what was probably the road along which a definite sporophyte generation became evolved, and which has led to the evolution of the higher plants, that are but highly organized and specialized sporophytes upon which the gametophytes have become dependent.

SPIROGYRA

(A.) The Thallus.

Spirogyra is another filamentous alga of the *Chlorophyceæ* that may be found floating upon the surface of stagnant ponds or slowly moving streams during the summer months. In mass it is of a dark green colour, slimy to the touch, and somewhat flocculent in appearance. If kept in an aquarium it will be seen that some portions of it are arranged in a vertical direction, and present a wavy outline; this habit is connected with its mode of reproduction, though by no means an essential part of it.

Examined in a drop of water beneath the microscope, the green mass is seen to be composed of a number of unbranched filaments, each of which consists of a number of cells (Fig. 140) arranged in a single series. Thus *Spirogyra*, like *Ulothrix*, is one of the simplest of multicellular plants. The surface of the filament is covered with a slimy material, said to be secreted by the protoplasm, and not to result from the alteration of the outer surface of the cell-wall. The cell-wall (Fig. 140, I) is firm and stratified, and composed of cellulose; the nature of the septa by which individual cells are separated varies

in different species: in some it is a single membrane, and in others a double one, the two layers of which are slightly separated from each other in the middle, and project slightly as a small involution into the cells. The protoplasm (P) forms an internal layer upon the cell-wall, sometimes called the 'primordial utricle,' which surrounds a large cell-vacuole containing cell-sap (CS). The nucleus (N) contains a large nucleolus, and is sometimes embedded in the 'primordial utricle,' and sometimes lies in the centre of the cell-cavity, invested in protoplasm, which is connected with the primordial utricle by radiating threads. The chloroplastids are of a special form; in all

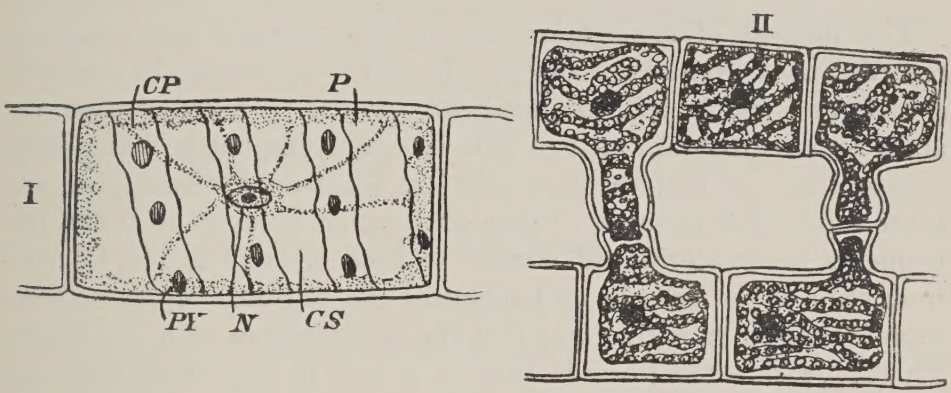


FIG. 140. *Spirogyra*. I. A single cell of a filament. CP=chloroplastid; CS=cell-sap; N=nucleus; P=protoplasm; PY=pyrenoid. II. A portion of two filaments conjugating. To the right the tubular outgrowths have met, but to the left their opposed walls have become absorbed, thus leaving an open channel between the cells of the two filaments. Magnified 300 times.

plants, with the exception of *Ulothrix*, which we have so far studied, they consist of more or less globular grains, but in *Spirogyra* they are of the form of spiral plates (CP) embedded in the primordial utricle; there may be one, or as many as six or seven, of these plates in each cell. Embedded at regular intervals in the chloroplastids are lenticular bodies of a proteid nature, called **pyrenoids** (PY). We have already learned that the starch grains are formed within the chlorophyll corpuscles; in *Spirogyra* their formation is limited to the immediate vicinity of the pyrenoids round which they are formed.

(B.) Methods of Reproduction.

(*a.*) Vegetative.

Spirogyra can reproduce by means of cell-division, which usually occurs between the hours of 10 p.m. and 12 p.m. In this process

the nucleus of the cell divides and forms two new nuclei which move apart; a septum then gradually extends inwards from the cell-wall, and meeting in the middle divides the original cell into two, each with a nucleus. Each may then grow to the size of the original cell, and thus bring about elongation of the filament. In other cases—those in which the transverse septum is double—the filament may separate in the plane of the new septum, and thus form two fresh filaments, each of which may elongate by the addition of new cells.

(*b.*) Conjugative.

The method of conjugation, as we have already seen, may be regarded as a primitive sexual act, in which the distinction between a male and female cell has not been attained. In conjugation, the act is so far sexual in that two cells fuse together, but it differs from a sexual act, in that the two cells are identical in form, size, and other appreciable features. When conjugation is about to occur, two filaments become arranged parallel to each other (Fig. 140, II), and from some of the cells in each filament the cell-wall begins to form a protuberance in such a way that the protuberance of a cell in one filament is directed towards that of a cell in the other filament; ultimately the two protuberances meet, and the opposed walls becoming absorbed an open passage is formed between the two cells. While this has been proceeding, the protoplasm of either cell becomes retracted away from the cell-wall and forms a rounded mass, that of one cell being in advance of the other. The more active of the two cells—that which is first rounded off, and which may be regarded as the male cell, since it is active while the other is passive—then begins to pass through the canal into the other cell, where it fuses with the protoplasm of that; not only does the protoplasm fuse, but also the two nuclei. Since all the cells in the same filament behave in the same way, we may distinguish between male and female filaments or individuals. In *Zygnema*, a closely allied alga, the protoplasm of both cells move into the connecting channel where they meet and fuse, so that both cells are absolutely identical, and the act is one of conjugation pure and simple. But in *Spirogyra* there is the first beginning of that differentiation between the sexual cells which reaches its highest expression in the spermatozoid and ovum. The coalesced mass formed by the fusion of the protoplasm of the two cells then becomes surrounded by a thick cell-wall, the outer

surface of which becomes cuticularized, and is then known as a zygospore. The zygospore does not germinate at once, but undergoes a period of rest after the conversion of its contained starch-granules into oil-droplets. In virtue of the cuticularized outer wall it can live through the winter or a period of drought.

The first external evidence of germination of the zygospore is the rupture of the outer wall ; at the same time the oil globules undergo an alteration, and are in part represented by starch grains, and the chlorophyll bands assume their bright green colour. The thin, cellulose inner wall, with the contents of the cell, now grows and begins to elongate ; in a very short time the hinder end of the growing plant becomes narrowed and colourless, and attaches itself to some substratum. Transverse cell-walls soon appear, and a filament of *Spirogyra* is thus formed. The colourless, elongated, basal part disappears, and the filament then floats free.

VAUCHERIA.

(A.) Structure of Thallus.

Vaucheria, like *Ulothrix* and *Spirogyra*, is a filamentous alga, but it differs from them in the absence of transverse septa, so that the filament is not divided up into distinct cells. It is also much larger, and its filaments (cœnocytes), which can be easily seen by the naked eye, form coarse tangled masses of a dark green colour. It lives in fresh water or on the surface of damp soil, and is a very common plant on the surface of fern-pots.

If we examine some of the filaments in water under the microscope, it will be seen that they repeatedly branch, a character in which they differ from those of *Ulothrix* and *Spirogyra*. Some of these branches are colourless and act as rhizoids, penetrating into the soil or mud. The filament is limited by a cellulose membrane, and within this is a layer of protoplasm, which bounds the central cell-sap. In the protoplasm are very numerous chlorophyll grains and oil drops; *Vaucheria* is somewhat exceptional among green-plants in possessing oil instead of starch as a reserve food-substance. By staining with methyl-green after dissolving out the chlorophyll, numerous nuclear bodies may be demonstrated, scattered in the protoplasm, so that, since the filament possesses no transverse septa, we may regard *Vaucheria* either as a multinucleated cell, or as a multicellular filament in which the transverse walls are not developed.

(B.) Reproduction.

Vaucheria reproduces sexually and asexually. The asexual process is a very simple one, for the protoplasm becomes aggregated at one end of the filament, which bulges out into a club-shaped form. The terminal portion then becomes constricted off from the rest of the filament by the formation of a transverse septum (Fig. 141, II). The protoplasm in the terminal cell contains numerous nuclei and chlorophyll grains. The terminal cell is a zoosporangium, and the multinucleated mass within a zoospore. The zoosporangium splits open at its free end and the zoospore swims out. The spore is then seen to be a naked mass of protoplasm (Fig. 141, III), ovoidal in form, and covered with cilia, arranged in pairs; each pair of cilia is related

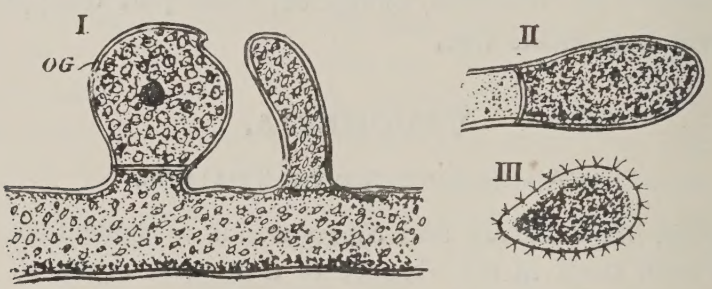


Fig. 141. *Vaucheria*. I. A portion of the filamentous thallus bearing an oogonium (OG) and an antheridium. II. The end of a filament, showing a zoosporangium. III. A liberated zoospore.

to one of the nuclei lying in a zone beneath the surface of the zoospore, in such a way that there is a pair of cilia for each nucleus.

The zoospore swims about for a short time, about half an hour, and then retracts its cilia and comes to rest. It germinates at once, by forming a colourless rhizoid which penetrates the soil, and a green filament which very soon branches and gives rise to a new *Vaucheria* plant.

The sexual mode of reproduction is resorted to when external conditions are unfavourable, especially when the level of the water in which the plant is living becomes low. The sexual reproductive organs are formed as lateral outgrowths of the filament, and may arise at any part of it. The oogonia or female organs (Fig. 141, I, OG) arise as globular outgrowths into which protoplasm from the filament enters; this protoplasm, like that of the thallus, contains numerous nuclei, chloroplastids and oil-drops. After a while, some of the protoplasm and all of the nuclei except one pass back into the

filament, and the oogonium then becomes cut off by the formation of a transverse septum from communication with the filament. The uninucleated mass of protoplasm within the oogonium is the **ovum**, and at the part near the beak it becomes clear, forming the receptive spot. At about the time that the ovum is formed, the oogonium forms a small sharp beak, which a little later splits open, thus forming a channel through which the spermatozoids may pass. At the time that the beak is split open, a small quantity of protoplasm exudes from it.

The **antheridia** or male organs arise at first like vegetative branches, but their position close to an oogonium indicates their reproductive nature. The antheridium becomes curved and bends towards the oogonium. Its protoplasm contains a large number of nuclei, and around each of these a thin film is formed which is prolonged at either end into a cilium ; these bodies are the spermatozoids, and they are liberated by the bursting of the antheridium, at the time that the oogonium is ripe. They swim through the interval that separates the perforated beak of the oogonium from the antheridium, and passing through the aperture, reach the ovum. One of the spermatozoids penetrates it at the receptive spot, and reaching the nucleus, fuses with it. The fertilized ovum then surrounds itself with a cell-wall and undergoes a period of rest. The oospore can resist a period of drought, but on the return of favourable conditions, it germinates at once and gives rise to a new *Vaucheria* filament.

Like *Ulothrix*, *Vaucheria*, if left stranded high and dry by the lowering of the level of the water, can protect itself by the filament splitting up into cells, each of which surrounds itself with a thick cell-wall ; in this condition the cells can live throughout a prolonged drought, and on the return of aquatic or other favourable conditions, they grow into *Vaucheria* filaments.

Vaucheria is thus characterized by its very simple vegetative structure, and by the absence of any definite alternation of generations. Notwithstanding its simple structure, it has reached a high grade in its reproductive organs, and possesses well-differentiated male and female cells (gametes). Both the sexual and asexual organs may be developed on the same plant, but it wholly turns upon external conditions. If the environment is favourable, the plant goes on generation after generation asexually and without the formation of sexual organs at all. It is only when unfavourable conditions appear that the sexual process of reproduction is resorted to. But in no

event is there any differentiation into a sporophyte and a gametophyte, the thallus being a sporophyte at one time, when conditions are favourable, and a gametophyte at another time, when the existence of the plant is threatened by adverse surroundings.

HÆMATOCOCCUS (PROTOCOCCUS).

(A.) Structure of the Thallus.

In passing down the scale of vegetable life, we have studied at the top, members of very great complexity of organization, made up of very diverse tissues and with a complicated life-history, and when we reached the algæ, we found the vegetative structure very much simpler, for in *Ulothrix* and *Spirogyra* the plant consists of a simple uniseries of cells, and there is no differentiation of tissue, all the cells having the same characters. We have now to study an even simpler plant, one which remains throughout life at practically what is the egg or spore-stage of higher forms, i. e. that of a single cell.

Hæmatococcus is so called on account of its red colour, but it none the less belongs to the green algæ or *Chlorophyceæ*, since it is really a green-plant, but in which the colour of the chlorophyll is more or less completely masked by the presence of a red cell-sap. It possesses a very wide geographical range, and like other very simple organisms can live under environmental conditions that would prove fatal to higher forms. In mountainous districts above the snow-line, and in Arctic regions, *Hæmatococcus* with a few species of Diatoms constitute the only plant organisms that can live under these conditions. To the presence of this plant the red colour of so called 'blood snow' is due. In temperate climates it lives in the mud, in puddles, and in the gutters of the roofs of houses.

If we spread out in water a very thin layer of mud that has a decided red colour (not due of course to the red oxide of iron), we shall find a large number of small, round, red bodies floating in it, about $\frac{1}{300}$ inch in size (Fig. 142, I). Careful examination will show that each one is a cell, with a well-marked cell-wall (C), enclosing a film of protoplasm and centrally a vacuole filled with cell-sap. The cell-sap is coloured with a dissolved red pigment, and it is to this that the red colour is due. Some of the individuals possess a more intensely red colour than others, while a few have a colourless cell-sap. If we examine these latter, we shall find that embedded in the protoplasm are a few relatively large chloroplastids (CH), and within each chloro-

plastid two or three pyrenoids, similar in nature to those present in *Spirogyra*. By special methods of staining—by decolourizing with alcohol and treating with methyl-green—the presence of a single nucleus (N) may be demonstrated.

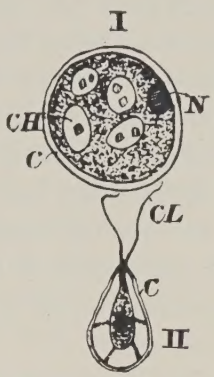


FIG. 142. *Hæmatococcus* (*Protococcus*) *pluvialis*. I. A single plant. II. A zoospore. Magnified 300 times. The zoospore is drawn on a larger scale than the plant. C = cell-wall; CH = chloroplastid; CL = cilia; N = nucleus.

Thus, *Hæmatococcus* is a plant composed of a single cell only, and yet notwithstanding its simplicity, it is capable of performing all the essential functions of the higher plants. In virtue of the possession of chlorophyll it can assimilate carbon from the carbon dioxide of the atmosphere, while its nitrogen and mineral salts it obtains from the nitrates and other salts in solution in the water in which it lives (cp. chap. XXIII on Assimilation). The complex structure of the higher plants, though necessary for the performance of their special functions, is not necessary for the manifestation of life. For this, in its essential features, the most simple structure is all that is necessary; in fact, a cell-wall is not required, but only the protoplasm and its nucleus, for as we shall see in a moment, the reproductive bodies of the plant exist for some time in the naked condition, and swim about as blebs of protoplasm.

(B.) REPRODUCTION.

The reproduction of *Hæmatococcus* is in most species, as far as is known, wholly asexual, by means of zoospores (Fig. 142, II). The protoplasm of the cell simply divides up and forms so many pear-shaped bodies with two cilia, each with a nucleus and a chloroplastid. There are two kinds of zoospores formed: the **macro-zoospores** and the **micro-zoospores**. The macro-zoospores are formed when the protoplasm of the cell divides into only two, four, or eight masses, and the microspores when it divides into sixteen, thirty-two, or sixty-four. In their activities and form, the two kinds are identical, and they only differ in their size. When first liberated they are pear-shaped naked masses of protoplasm, with two vibratile cilia attached at their narrow end. By the lashing of the cilia, the zoospores are propelled through the water. They are very sensitive to the influence of light, and like the zoospores of *Ulothrix*, they avoid and swim away from direct and bright light, and swim towards diffuse and moderately

intense light. After they have swam about for some time in the naked condition, they surround themselves with a cell-wall (Fig. 142, II, c), which does not, however, closely invest the protoplasm of the cell, but leaves a cavity, filled probably with a cell-sap, and traversed by a few strands of protoplasm, passing from the cell to the cell-wall. Shortly after this, they retract their cilia and come to rest, and each zoospore becomes a fresh individual *Hæmatococcus*. In some species, a process of conjugation has been observed. Two of the macro-zoospores while in the naked condition meet and interlace their cilia, and gradually the substance of the two spores merges. The body thus formed is a zygospore; it becomes surrounded by a cell-wall and gives rise to a new plant.

The life-history of *Hæmatococcus* thus consists of a **resting** and a **motile stage**. The resting stage is the vegetative one, and the motile stage is the reproductive one.

CHAPTER XV

(*b.*) THE FUNGI.

THE fungi form the largest class of cryptogamic plants, and alike from an academic and economic point of view is an exceedingly interesting and important one. The life-history of many of them is still unknown, and it is probable that several which are now regarded as distinct species are but different stages in the life-cycle of a single form.

Their economic importance can be understood from the fact that the diseases of timber, both as a constituent of the living tree and as the manufactured article, and the diseases which attack cereals, silkworms, and grape-vines, are due to them. In fact, there is not an industry which derives its raw materials from organic sources that has not suffered heavy financial loss from diseases of which fungi are the cause; in some cases, as in the potato-blight, the silkworm disease, and the destruction of grape-vines, the loss has been so great that it has amounted to a national one. It is thus obvious that a complete knowledge of the life-history of these forms, which is sometimes very complex, and an intimate acquaintance with the conditions necessary

for their existence, is of the greatest economic importance, if invested capital and labour are to obtain a full return.

From an academic point of view, their morphology and life-histories are no less important and interesting. Some of them, in respect of these characters, show a very close affinity to certain of the algæ, and suggest that the two great classes have arisen from a common origin. All the fungi[1] are characterized by the common physiological feature of the absence of chlorophyll and starch, and in virtue of the affinities above mentioned, we may regard them as degenerate algæ which have lost their chlorophyll and the consequent power of obtaining the carbon of their food from such a simple source as the CO_2 of the atmosphere; they have, therefore, to seek it either from the organic matter of decaying substances, when they are called **saprophytes**, or from the tissues of living organisms, both animals and plants, when they are called **parasites**. The toadstools (mushrooms) and moulds are familiar examples of saprophytes, and the smut and rust of wheat, and the bacteria of infectious diseases, are examples of parasites.

All fungi[2], in respect of their life-histories, are characterized by the development from the spore of a filamentous structure called a **mycelium**, which may be unbranched, but is usually profusely branched, and which ramifies among the substratum from which it obtains its nutriment; this is the vegetative phase of the life-cycle, and upon it the reproductive organs or fructification are borne. In a large number of fungi an 'alternation of generations' has been discovered, and it is possible that as investigation of other forms proceeds, a similar alternation of an asexual with a sexual generation will be established.

(*a.*) Basidiomycetes.

THE MUSHROOM (*Agaricus Campestris*).

The Basidiomycetes include the largest and most beautiful of the Fungi, and are characterized by the large size and comparatively complex structure of the fructification, and by the origin of the spores from special elements of the nature of single cells, called **basidia**.

That which is commonly known as the mushroom is the fructification of the plant, the vegetative mycelium being of insignificant proportions

[1] With the exception of three species of bacterium.

[2] Certain bacteria and Myxomycetes—if this latter is to be regarded as a plant—excepted.

and remaining within the decaying mass, such as manure or leaves, upon which the plant lives. The brick of 'mushroom spawn,' which can be bought from horticultural dealers, consists of a compost of manure mixed with the mycelial filaments of the plant; if this compost be kept at a sufficiently high temperature, in a moist atmosphere and in the dark, mushrooms (the fructifications) will develop from it.

Examination of teased portions of such a compost beneath the low power of the microscope will reveal a number of whitish strands (Fig. 143, M), forming a more or less dense network, some of which are sufficiently thick to be visible to the unaided vision, while others are only just visible beneath the low powers of the microscope; the former of these are strands composed of a large number of the latter, arranged parallel to form a bundle. The smallest of these strands are the individual filaments or **hyphæ**, each of which branches freely and is divided at irregular intervals by transverse septa; the compartments thus formed contain protoplasm, oil globules, and several nuclear granules, so that we may regard each hypha as being a multicellular filament, composed of multinucleate cells. Frequent fusions between contiguous filaments take place, comparable to the processes of conjugation in *Spirogyra*, but here having nothing to do with reproduction, and are probably alone concerned with facilitating nutrition. The walls of the filaments consist of some modification of cellulose, called fungus-cellulose, since it does not stain blue with iodine and sulphuric acid, or with Schultze's solution, until after it has been treated with caustic potash, by means of which probably some nitrogenous matter is extracted.

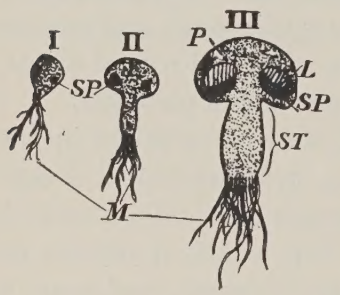


FIG. 143. Developing ructifications of the Mushroom (*Agaricus campestris*). L=hymenial lamella; M = portion of mycelium; P=head or pileus; SP=circular canal; ST=stipes or stalk.

The vegetative phase of the life-cycle of *Agaricus* thus consists of a closely woven, branching mycelium, ramifying among the material from which it obtains its nutriment. The reproductive portion, or the fructification, arises from this as a little nodular body composed of hyphæ so closely woven that, seen in section with the unaided eye, they appear as homogeneous masses of white tissue (Fig. 143, I). In some of the larger of these masses (button mushrooms), a distinction into a head (P) and a stalk (ST) can be discerned, and running round

the periphery of the former there is a somewhat circular canal (SP), in which, later, the so-called 'gills' (L) will be formed. In older specimens (III) this canal becomes enlarged, and its floor very thin; from its roof, radiating blade-like downgrowths (L) develop, which dip down into the cavity of the canal, and constitute the rudiments of the gills or **hymenial lamellæ**. As the head or **pileus** (P) enlarges and expands circumferentially, the floor of the canal, now called the **velum partiale**, is ruptured, but its attachment to the stalk or **stipe** persists throughout as a fringe of withered tissue, called the **annulus**; the rupture of the velum partiale exposes the hymenial lamellæ, which may be seen upon the under surface of the pileus as radiating, closely set, vertical plates. It is upon the hymenial lamellæ that the asexual reproductive bodies, the **spores**, are borne, and if a mature pileus be laid upon a sheet of paper and allowed to remain for a few hours, upon its removal thousands of spores will be found deposited upon the paper; these have fallen from the surfaces of the lamellæ, and are arranged in radiating lines which correspond to the spaces between the lamellæ. Microscopically examined, the stalk or stipe is seen to be composed of a large number of hyphæ running more or less parallel to each other, and more densely packed in the periphery than in the central portion of the stalk. The individual hyphæ are branched and divided at short intervals by obliquely-arranged transverse septa; the protoplasm is not copious, forming a thin layer upon the inner surface of the cell-wall, and enclosing a central vacuole or vacuoles of oil; in the protoplasm of each cell there are several small nuclei.

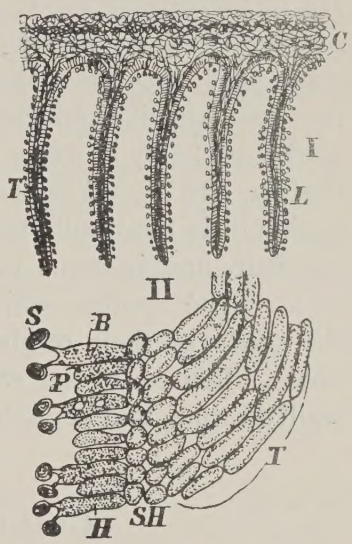


FIG. 144. **I.** Tangential section through the 'head' or pileus of *Agaricus*. C = hyphæ of the pileus; L = hymenial lamella; T = trama. Magnified 80 times. II. A small portion of a hymenial lamella. Magnified 300 times. B = basidium; H = hymenium; P = paraphyse; S = spore; SH = sub-hymenium; T = trama.

The hyphæ of the stipe pass upwards and expand into the mass of hyphæ composing the pileus, which are here much branched, and form a network of filaments (Fig. 144, I, C); otherwise the hyphæ are similar to those of the stipe. At the surface of the pileus the hyphæ are more closely woven, so as to give the surface a somewhat greater

density than the bulk of the tissue within. The hyphæ which pass downwards and form the hymenial lamellæ (L) are differentiated into a central and a peripheral layer: the central portion called the **trama** (T) is composed of filaments which run longitudinally, and towards their free extremities turn outwards to the surface of the lamellæ, and bear short squarish or ovoidal cells (SH), which constitute a layer of pseudo-parenchyma, called the **sub-hymenial layer**; the peripheral layer, called the **hymenial layer** (H), consists of elongated, somewhat club-shaped cells, borne upon the sub-hymenial layer, and of which two types are to be distinguished: shorter, narrower cells, the **paraphyses** (P), and more bulky and longer ones, the **basidia** (B). The latter are the spore-producing cells, the **spores** (S) being developed at the end of two little peg-like processes, the **sterigmata**, while the former remain sterile, probably in some way contributing to the nourishment of the basidia. In *Agaricus* the number of sterigmata developed from each basidium is constantly two, but in other mushrooms (*Coprinus*) they are four, and in some of the Gasteromycetes there are as many as eight. The spores—which are called **basidiospores** on account of the mode of their origin—are exceedingly minute, dark, unicellular bodies, limited by an external, thicker extine, and an inner, thin-walled intine, and containing globules of oil in their protoplasm.

Germination of the Spores.

The conditions necessary for the germination of the spores of *Agaricus* have only been recently discovered, all previous attempts at germination in artificial media having failed. It has been found that germination will take place upon wood which has been treated for some time with nitric acid and then washed in water. The extine bursts, and the intine grows out at two or more points as a hyphal filament.

(β) Phycomycetes.

(I) Oomycetes.

The Phycomycetes, to which *Pythium* belongs, is of great scientific interest on account of the fact that the morphological characters of the genera belonging to it are very similar to those of the class of algæ to which *Vaucheria* belongs.

PYTHIUM.

The mycelium of *Pythium*, unlike that of *Agaricus*, lives upon the tissues of living plants, and is therefore a parasite. It is the cause of the 'damping off of seedlings,' a phenomenon of common experience to gardeners, and which may be produced at any time by sowing cress seedlings in a very damp atmosphere. The mycelium developed from the spore penetrates the stem of the seedling, either through a stoma or by dissolving a path before it, through the cuticle and epidermis; the tips of the mycelial filaments possess the power of secreting a digestive fluid or enzyme, which dissolves the tissues of the host-plant, and thus the parasite can journey through any portion of the tissues of the host, and utilize the dissolved materials as food.

The mycelium consists of irregularly branched hyphæ, which are not divided by transverse septa, so that it partakes of the nature of a much-branched and elongated single cell. The contained protoplasm is vacuolated, the vacuoles containing oil, and embedded within it are numerous nuclear granules.

Reproduction.

(*a*) Asexual.

The asexual methods of reproduction are by two modes, i.e. by means of **conidia** and **zoosporangia**. The conidia are spherical bodies formed at the end of filaments or at any part along the hypha; in either case they contain granular protoplasm, which is constricted off from that in the hypha by means of a septum. The protoplasm of a conidium grows out through a rupture in the wall, and directly forms a new mycelium; the essential characters of conidia are that they are spores produced by bud-like constrictions of part of a hypha, and which germinate directly into a new mycelium. The zoosporangia (Fig. 145, z) are spherical bodies, usually produced at the termination of a hypha which has grown out from the host-plant into the air, and which bear little beak-like projections. The spherical part of the sporangium contains a granular protoplasm, constricted off from the hypha by a septum; the protoplasm passes out into the beak, which enlarges until it is large enough to contain the whole of the protoplasm. The protoplasm then becomes constricted into a number of small, oval, biciliate bodies, the **zoospores** (zs), which are liberated, and after a period of active locomotion by the action of their cilia they come to

rest, and subsequently germinate, producing a new mycelium. The essential characters of zoospores are that they are formed by the division of a mass of protoplasm, and that they are capable of free locomotion by means of cilia.

Asexual reproduction by means of conidia is one adapted to terrestrial conditions, while that by means of zoospores is adapted to an aquatic state, though on account of the extreme smallness of the motile spores, a film of moisture, such as would be present on seedlings on a damp day, is sufficient for the purpose. Reproduction by means of zoospores is a very effectual and rapid one, but is wholly dependent upon the presence of moisture; hence the term 'damping off' applied by gardeners to seedlings attacked by *Pythium* or its allies, since the disease is most prevalent and spreads most rapidly in very damp weather, or in propagating pits kept too moist.

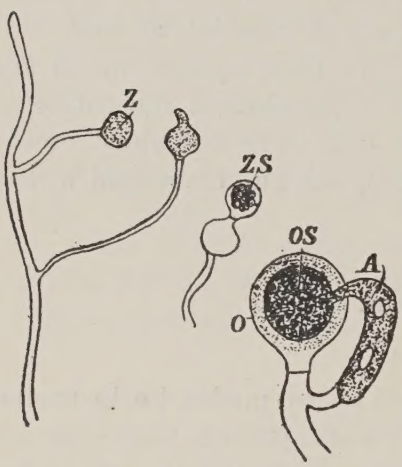


FIG. 145. Reproduction of *Pythium*. A=antheridium; O=oogonium; OS=oosphere or ovum; Z=zoosporangium developing; ZS=zoospores.

(*b*) SEXUAL.

The sexual organs (Fig. 145) may be borne upon hyphæ which are within or without the host-plant, and either at the termination of a hypha or at any part along it. The female organ is an **oogonium** (O), and is formed as a spherical outgrowth from the hypha, and into it a large portion of the hyphal protoplasm passes, which is retained in the oogonium by the formation of a septum between it and the hypha. At first the protoplasm is uniformly granular, but it ultimately becomes divided into a central granular portion, probably containing only one nuclear granule, and a peripheral clearer portion, with many nuclear granules; the former is the essential portion and is called the ovum or **oosphere** (OS), while the latter is the **periplasm**. The male organ or **antheridium** (A) is of the nature of a hyphal branch, and may arise upon the same hypha as the oogonium, or upon a different one. It is a more or less club-shaped, lateral outgrowth, which becomes constricted from the hypha by the formation of a transverse septum; its protoplasm also becomes divided into a central granular and peripheral portions. The

antheridium bends towards the oogonium, and sends out a very short, cylindrical tube, which pierces the oogonial wall, and through which the granular protoplasm of the antheridium passes to fuse with that of the oogonium.

After fertilization the oosphere surrounds itself with a cell-wall and becomes the **oospore**. The oospore is a resting body and does not germinate at once, and only when brought into contact with water. There is considerable variation in the mode of germination, dependent upon the abundance or scarcity of food material; if this be abundant, a new plant (mycelium) is produced, but if scarce, then the life-history is lengthened and the formation of the mycelium is postponed. When the mycelium is formed at once, the outer layer of the spore wall bursts and the protoplasm invested by a thin wall grows out and forms a filament, which by branching produces a mycelium. The first-formed filament, however, may be very short, and may give rise to a sporangium into which the whole of the protoplasm passes, and dividing into small masses, forms zoospores. Or, the zoospores may be formed within the oospore, not even the commencement of germination taking place. The object of the formation of zoospores under unfavourable conditions is, by virtue of the migratory nature of the zoospores, to increase the probabilities of food material being found.

Thus, under unfavourable conditions, *Pythium* may exhibit a not well-defined 'alternation of generations,' inasmuch as the sexual organs may produce a rudimentary spore-bearing hypha, which never gives rise to sexual organs. From the spores derived from this a mycelium is produced, which, though it may develop asexual organs in its earlier stages, ultimately produces oogonia and antheridia. But so long as food-material is abundant, an 'alternation of generations' is not represented.

The life-history of *Pythium* then, briefly summarized, is as follows:—from the vegetative mycelium, an earlier spore-producing stage is developed, from which arise spores (conidia or zoospores), and which give rise at once to a new mycelium. From the same mycelium a later sexual organ-producing stage is developed, from which results an oospore; this may give rise, according to circumstances, either to a new mycelium, or it may, as it were, hark back to a spore-producing stage, by developing a hyphal filament bearing zoosporangia, or it may not lengthen the life-cycle quite so much, and produce zoospores directly.

(2) Zygomycetes.

MUCOR MUCEDO.

Pythium is a fungus which exhibits a very definite sexual act of reproduction, so it is placed in the sub-class Oömycetes of the class Phycomycetes. As already indicated the members of the class exhibit, in virtue of non-septate hyphæ and in their general life-history, a resemblance to the class of algæ to which *Vaucheria* belongs. But while some of them, like *Pythium*, produce sexual organs, others, like *Mucor*, our next type, form conjugating organs, from which a zygospore results, and are placed in another sub-class, the Zygomycetes.

(A.) Structure of the Mycelium.

Mucor lives on damp bread and horse-dung, and may be easily obtained by placing a little bread in a damp and dark place. The mycelium is white and flocculent in appearance to the naked eye, and in about four or five days little black dots appear on the end of some vertical filaments. The black dots are spore-cases or sporangia. The mycelial hyphæ are similar to those of *Pythium*, and are long, branching, non-septate, multinucleate filaments or **cœnocytes**. Some of the hyphæ penetrate the substratum and absorb nutriment, while others radiate out in all directions, seeking for fresh fields of nutritive substance.

(B.) Reproduction.

(*a*) Asexual.

Some of the hyphæ rise up vertically above the mycelium, and their extremity swells out into a globular head (Fig. 146, S). The vertical hypha is called a **gonidiophore**, and the swollen sac at its end becomes a **sporangium** (S). Soon after its formation the protoplasm within the developing sporangium becomes cut off from the hypha by the formation of a transverse cell, which at a later period becomes pushed up into the sporangium as a column-like body, called the **columella** (C). Meanwhile the protoplasm of the sporangium becomes constricted into a large number of uninucleated masses, the **spores**. At the same time, the wall of the sporangium becomes brittle and black by the deposition within it of crystals of calcium oxalate, and a mucilaginous substance is formed among the spores. When the

sporangium is quite ripe, the mucilage absorbs water, swells, and bursts the sporangium wall, and at the same time liberates the spores.

The spores germinate at once, by growing out as a single filament, which very soon branches and rapidly grows into a new mycelium.

(*b*) Conjugative.

When conditions are unfavourable to rapid growth, such as a falling off in the amount of food material or a lessening in the degree of moisture, *Mucor* resorts to a process of conjugation. Two filaments, adjacent to each other, rise up above the mycelium and approach one another; the extremity of each then swells, and presently these swollen parts come in contact (Fig. 146, z); a little later and the septum separating them becomes absorbed, and the protoplasmic contents then merge. The resulting body is a **zygospore**, since we have here a typical act of conjugation. The zygospore grows immensely, and its wall becomes very thick. It then undergoes a period of rest. If it should be blown or otherwise carried to a suitable environment, it germinates and forms a new mycelium. But if food is not very abundant and other conditions are unfavourable, it forms a short hypha only, and upon this an asexual sporangium is formed, thus increasing the chances of finding a suitable habitat.

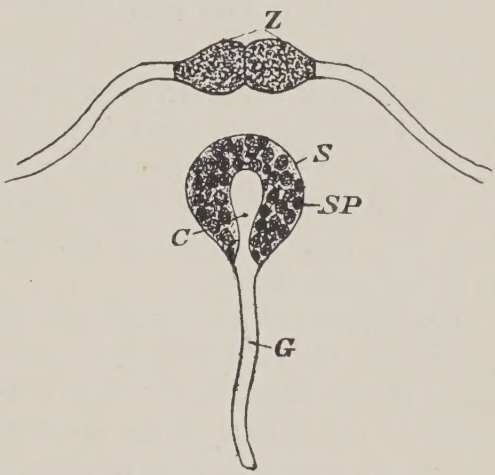


Fig. 146. Reproduction of *Mucor mucedo*. C=columella; G=gonidiophore; S=sporangium; SP=spores; Z=zygospore in course of formation. Magnified 300 times.

Mucor is more adapted to a terrestrial mode of existence than *Pythium*, because its asexual spores are distributed wholly by air-currents, whereas those of *Pythium* depend upon water for their transference from one place to another. Most fungi reproduce asexually by means of air-borne spores, so that the water-borne zoospores of *Pythium* is an exceptional feature among fungi; but it is very characteristic of algæ, which do not depend at all upon the wind for the dispersion of their spores.

(γ) Ascomycetes.

The Ascomycetes are a group of fungi characterized by the presence of sac-like outgrowths, called **asci**, from the female organ of reproduction, and in which a few but definite number of spores, called **ascospores**, are formed. The hyphæ of all ascomycetes are septate, so that they are multicellular. We shall study one of the moulds, technically known as *Eurotium aspergillus glaucus*, which is very common on stale bread that has been kept in a damp and dark place.

EUROTIUM ASPERGILLUS GLAUCUS.

(A.) The Structure of the Mycelium.

If we examine the surface of a piece of damp bread that has been kept in a dark cupboard for a few days, we shall find that it becomes covered with a felted mass of white filaments; this is the mycelium. A little later tufts of a greenish colour appear; these are the organs of asexual reproduction. Later still, little yellow blebs appear scattered here and there; these are the **cleistocarps**, enclosing the organs of sexual reproduction.

The hyphæ are long, branched, septate filaments, containing protoplasm and oil vacuoles; each cell contains many nuclei, though in some of the allied forms there is but a single nucleus in each cell. Some of the hyphæ of the mycelium penetrate the substratum and absorb the nutriment from it, while others spread out in all directions, seeking for fresh nutritive surfaces, as the old becomes exhausted. Sooner or later, the whole of the nutritive matter becomes used up, and the plant must adopt some method by means of which its progeny can arise in places where fresh food material may be found. And to attain this some of the branches rise vertically upwards, and at their extremities reproductive spores are formed. The mode of formation of these we must now study.

(B.) The Reproductive Organs.

(*a*) Asexual Organs.

The extremity of one of the vertical branches (Fig. 147, C) swells and becomes nearly spherical; this vertical branch is the **conidiophore**. From the spherical swelling at the end of the conidiophore, there arise a large number of finger-like processes, called **sterigmata**

(S). These later become constricted into a row of beads, each bead of which contains a single nucleus. The process of constriction ultimately proceeds so far that the beads become separated from each other by the slightest breath of wind, and are so dispersed away from the parent plant. These beads are spores; and spores which are formed by the constriction of a filament are called **conidia.** If they alight on a suitable substratum, under suitable conditions, each conidium germinates by growing out into a number of filaments; each of these grows rapidly and branches, and a new mycelium arises. A mycelium is a mass of hyphæ derived from a single spore.

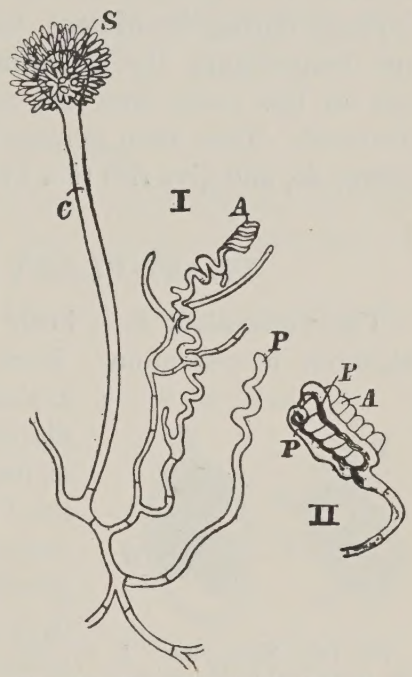


FIG. 147. Reproduction in *Eurotium aspergillus glaucus.* Magnified 300 times. A=ascogonium; C=conidiophore; P=pollinodium or antheridium; S=sterigmata.

(*b*) SEXUAL ORGANS.

The sexual organs consist of a spiral vertical hypha, called the **ascogonium** (Fig. 147, I and II, A), which arises as a branch of one of the hyphæ of the mycelium, and of an **antheridium** or **pollinodium** (P), also vertical, but only slightly spiral, and arising from one of the mycelial hyphæ. The pollinodium comes into close relation with the ascogonium, and the apex of the two organs meet. It has recently been shown that the walls in contact become absorbed, and that the protoplasm of the pollinodium passes over into that of the ascogonium. This therefore is a true sexual act, in which the distinction between male and female organs is very marked. After fertilization, the ascogonium becomes divided into several compartments by the formation of transverse walls; from each compartment a club-shaped sac arises, and into this the protoplasm passes. This sac is called the **ascus**, and soon after the protoplasm has passed into it, it becomes divided off from the ascogonium by the formation of a transverse wall. Its protoplasm then constricts into eight spores, which are called **ascospores**, because they are formed in asci.

While these changes are going on, several filaments arise from the base of the sexual organs, and growing upwards, form a dense, globular, wefted mass around them. The walls of the outer layers of this investment of filaments become thickened, and secrete a yellow waxy material. This globular sac is called the **perithecium**, and the whole thing, including the contained organs, is called a **cleistocarp** or 'closed fruit.'

The cleistocarp protects the ascopores from the influence of unfavourable conditions, and thus enclosed the spores can remain dormant during the winter. Under favourable conditions of moisture and temperature, the cleistocarp bursts by the absorption of water, and at the same time the asci are ruptured, and the ascospores liberated. They then germinate in the same way that the conidiospores do, and give rise to a fresh mycelium.

YEAST-PLANT (*Saccharomyces Cerevisiæ*).

The yeast-plant is a lowly fungus concerned in the processes of alcoholic fermentation. Each individual plant, called a **torula**, is a single cell (Fig. 148) about $\frac{1}{100}$ mm. in diameter, invested by a very thin wall (C) of fungus-cellulose, within which is a vacuolated protoplasm (P), some of the vacuoles containing oil (O). A definite nucleus is not present, though by the employment of certain dyes a nuclear-like granule may be discerned embedded in the central portion of the protoplasm.

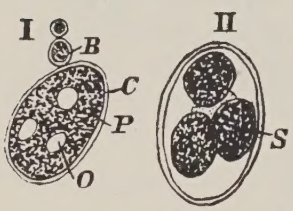


FIG. 148. Yeast-plant. I. An individual budding. B = bud; C = cell-wall; O = oil vacuole; P = protoplasm. II. Formation of endospores (S).

When food-material is abundant, yeast multiplies very rapidly by the simple process of **gemmation**, which is a form of fission. The protoplasm of the cell grows out as a minute bud (B), pushing the cell-wall before it; this bud gradually enlarges and ultimately becomes constricted off from the parent cell. It then grows until it attains the size of an adult cell, when it may repeat the process of gemmation. Very frequently, before the first gemmule has separated from the parent cell, another develops upon it, and even another upon the last, so that a temporary colonial condition is produced; but all the gemmules ultimately separate.

If food-material is scarce, or if the yeast-plant be starved by

placing it on a slab of plaster of Paris and covered by a bell-jar so as to ensure a continually moist atmosphere, it will resort to another mode of reproduction, i.e. that of **spore formation**. The protoplasm becomes much vacuolated, and more than the usual amount of oil appears; it then contracts away from the cell-wall, and divides simultaneously into four masses, arranged tetrahedrally, each of which becomes surrounded by a thick cell-wall (Fig. 148, S). The spores thus formed can withstand adverse circumstances, such as a high temperature, drought, and absence of food-material, to an extent that would kill the ordinary cell. But under favourable conditions each spore grows and becomes a torula.

The Physiology of Yeast.

The activities of yeast and the conditions under which they can best proceed have been investigated in great detail, so that we shall consider them somewhat fully.

If a small quantity of yeast be placed in a solution[1] containing the following ingredients,

Water, H_2O	83·76 per cent.
Cane-sugar, $C_{12}H_{22}O_{11}$ . . .	15·00 „
Ammonium tartrate, $(NH_4)_2C_4H_4O_6$	1·00 „
Potassium phosphate, K_3PO_4 . .	0·20 „
Calcium phosphate, $Ca_3(PO_4)_2$.	0·02 „
Magnesium sulphate, $MgSO_4$ . .	0·02 „

it will multiply very rapidly, as is evidenced by the turbid appearance of the liquid, and as may be seen by examination of a drop of it beneath the microscope. At the same time gas bubbles are disengaged from the surface of the liquid, while the substance of the liquid itself undergoes considerable changes. If the gas be collected and analysed, it is found to consist of CO_2; and if the liquid be distilled, the distillate is found to consist of alcohol. Hence, concurrently with the multiplication of the yeast-plant, the sugary solution is decomposed into carbon dioxide gas and alcohol. Is this presence of the yeast-plant a coincidence, or a real expression of the part it plays in the process? If precautions be taken to ensure that stray particles of yeast do not gain access to such a liquid, and if yeast which has been boiled and thus killed be added to it, alcoholic fermentation will not take place.

[1] This solution is that recommended by Pasteur and named after him.

And, moreover, from crushed yeast a soluble principle may be extracted, which upon addition to a sugary solution induces fermentation; to this substance, which belongs to a class of bodies called **ferments**, and which are capable of producing changes in other substances without themselves undergoing change, the name of **zymase**[1] has been applied. It is thus certain that alcoholic fermentation of a sugary solution is brought about by the activity of living yeast-cells, and that they accomplish this by the formation of a minute quantity of zymase. As to whether the ferment is secreted from the cells and the fermentation proceeds in the liquid outside them, or whether the liquid is absorbed by the cell and the products of fermentation excreted by them, is at the present moment a matter of conjecture.

Yeast can live and ferment in the absence of oxygen, though its growth is not vigorous and the amount of sugar decomposed is small; nevertheless, the weight of sugar transformed per unit weight of yeast is very great, i. e. 150 to 200 of sugar : 1 of yeast. In the presence of a limited amount of oxygen the growth of the torulæ is more vigorous and the fermentation proceeds more rapidly, but the quantity of sugar transformed per unit weight of yeast is much less, i. e. 60 to 70 of sugar : 1 of yeast. In the presence of a still greater quantity of oxygen, the growth of the yeast is very vigorous, but the sugar is oxidized rather than decomposed, the amount of alcohol which is formed being very small; and the amount of sugar which disappears per unit weight of yeast is also small, i. e. 4 to 6 of sugar : 1 of yeast.

Thus the presence of oxygen is favourable to the growth of the plant, but unfavourable to fermentation. Moreover, since the plant can live in the absence of oxygen, it probably possesses the power of extracting it from its combination with the hydrogen and carbon of the sugar.

Accurate analysis of the products of fermentation of a sugar liquid of known composition has shown that the following substances in the proportions given are produced:—

Alcohol and CO_2 . . . . 95 per cent.
Glycerine and succinic acid, 4 ,,

There is thus one per cent. of the sugar to be accounted for. If we remember that during the process of fermentation the yeast-plants

[1] For further details concerning zymase and ferments generally, cp. chap. XXIII, p. 451.

increase, it is easy to conceive that the unaccounted for one per cent. is used as nutriment for the living cells.

If the cultivation of living yeast-cells be conducted with Pasteur's solution, from which ammonium tartrate is excluded, the yeast-cells neither grow nor multiply. Neither will they live in the absence of potassium and calcium phosphates, although the smallest traces of these substances are all that is required. The presence of sugar is not absolutely essential to the life of the organism, since it can grow and multiply, though only slowly, in the absence of it.

Saccharomyces cannot obtain the necessary nitrogen with which to build up its protoplasm from simple nitrates such as green-plants can, but needs the somewhat more molecularly complex ammonium tartrate; moreover, if a still more complex nitrogenous body, such as peptone, be substituted for the tartrate, the yeast-plant flourishes better.

The activities of *Saccharomyces* proceeds most vigorously at a temperature between 28° and 34° C.

If a quantity of yeast is burnt, it at first chars, and finally CO_2, nitrogen, water, and SO_2 in the form of gases, are liberated. Ultimately nothing is left but a small quantity of white ash, which upon analysis is found to contain potash, lime, magnesia, and phosphoric acid. Hence the chemical composition of yeast explains the necessity for the presence of all the constituents (sugar excepted) in Pasteur's solution. The substance of yeast contains all the elements which are present in that, and hence if new yeast-plants are to arise, the necessary constituents must be present in the nutritive solution. The exact part which lime and potash play is not yet understood, and it seems remarkable that substances which are only present in such minute quantities in the substance of yeast, are so important that their absence renders life impossible.

(δ) Schizomycetes (Microbes or Bacteria).

We have already learned that when a solution of sugar (supra, p. 267) is left exposed to the air, it will, sooner or later, undergo fermentative changes, which are the result of the activity of a minute living organism, the torula or yeast-plant. And similarly, any organic substance when left exposed will undergo the same process of fermentative change. Fermentation is a definite chemical change produced within a substance by the action of some body which does not itself undergo change in the process. We speak of these bodies

as ferments, and they may be classified into two groups: the **organized** and **unorganized ferments**. The latter class contains bodies like ptyalin and pepsin, which are the active principles in salivary and gastric digestion respectively, and like the diastase of plants; with these we are not now concerned. The organized ferments are living organisms like yeast and bacteria. It must be borne in mind, however, that the unorganized ferments are derived from living cells, but their action is independent of the presence or influence of the cells which form them; and the distinction is one of convenience rather than one expressive of any real difference.

The chemical processes that result in organized fermentation are the outcome of the action of minute organisms called **microbes** or **bacteria**, and are set going very much in the same way that the yeast-plant produces the alcoholic fermentation of a sugary solution (supra, p. 267). The microbe secretes a body called a ferment or **enzyme** (pp. 268 and 451), which acts in a physico-chemical manner upon the substance in which the microbes are contained, and starts those series of changes that finally results in its conversion into other bodies. The infectious and contagious diseases, and many other diseases also, are due to fermentative changes produced in the blood or living tissues of organisms by the agency of bacteria. The substances which they form when acting on the blood or other tissues are called **toxins**, and are exceedingly poisonous; and the symptoms of disease are due to the effect of these poisons upon the organism.

The chemical changes which take place in fermentation have been illustrated in the case of yeast (supra, p. 268) and may be supplemented by a few examples in which the organized ferment is not yeast, but some specific microbe. Every one is familiar with the production of vinegar from alcoholic liquids; this fermentation, known as the acetic acid fermentation, is due to the presence of at least two species of microbes, i. e. *Bacterium aceti* and *B. Pasteurianum*, in the alcoholic mother-liquid. There are two stages in the process, in the first of which the alcohol is decomposed and oxygen is absorbed and aldehyde and water formed; in the second stage the aldehyde becomes oxidized into acetic acid. Chemically represented it may be stated thus:—

	Alcohol.		Oxygen.		Aldehyde.		Water.
First Stage	C_2H_6O	+	O	=	C_2H_4O	+	H_2O.

	Aldehyde.				Acetic acid.
Second Stage	C_2H_4O	+	O	=	$C_2H_4O_2$.

Another instance of fermentation is that familiar to every one, i.e. the souring of milk. This is produced by a specific organism, the *Bacillus acidi lactici*, which splits up the milk-sugar into lactic acid, and that gives to the milk the acid taste when it turns sour. It may be represented chemically thus :—

Sugar. Lactic acid.

$$C_6H_{12}O_6 \text{ (by simple decomposition)} = 2\,C_3H_6O_3.$$

While the disease-producing or **pathogenic** bacteria are harmful to man, many of the non-pathogenic forms are necessary and useful to him, and were bacteria as a class exterminated, the face of animate nature would be entirely altered. For man lives upon the lower animals, and carnivorous animals live by preying on herbivorous ones, and these latter live on green-plants, and they in their turn on the CO_2 of the atmosphere and some of the mineral constituents of the soil. Under present conditions the CO_2 extracted from the air by plants, and in the long run utilized to form the tissues both of animals and plants, is given back to the atmosphere when putrefaction of the tissues of dead organisms takes place. But this putrefaction is the result of bacterial action, and if it did not occur, the CO_2 of the atmosphere would become exhausted; green-plants would then starve for the want of one important constituent of their food, and with the destruction of the last green-plant the source of the food-supply of herbivorous animals would disappear, and they would perish, and with them the carnivorous animals and man, who derive their food from them. Certain of Pasteur's experiments also show that bacteria are useful in that they aid the germination of plants, and that if seedlings are grown in soil deprived of bacteria, germination is retarded. And there is reason to believe, too, that the digestion of proteids in the alimentary canal of man and other animals is in part brought about by the action of certain microbes, which transmute the albumins into peptones.

The phosphorescence of decaying fish and meat, exhibited under certain conditions, is due to the action of a form of microbe, known as micrococcus. Other forms of micrococci produce vividly coloured patches on the substance infected by them. Thus *Micrococcus prodigiosus* gives rise to brilliant purple patches on bread, milk, paste, meat, and other substances, when exposed in the dark to a damp heat. Other species of *Micrococcus* produce various other colours on different articles of food ; thus *M. aurantiacus* turns bread and eggs a bright orange colour ; *M. cyanus* is the cause of a beautiful azure blue colour on milk and other dietary articles; *M. chlorinus* produces a grass-

green colour; *M. violaceus* is violet and *M. fulvus* is rust-coloured; and *M. candidus* produces white patches on cheese. Another genus of microbe, i. e. *Bacterium*, also possesses several coloured species: *B. xanthinum* gives a yellow colour and *B. cyanogenum* a blue colour to infected milk. The dark green colour sometimes seen on badly baked bread, which has been kept for several days in a damp warm atmosphere, is due to the presence of *Bacterium ærugineum*.

In structure, microbes are very simple and consist of single cells of exceedingly small size, averaging from $\frac{1}{1000}$ to $\frac{5}{1000}$ of a millimetre in length. They vary much in their form, and some of them probably have different forms at different stages in their life-history. Each individual is exceedingly simple, and consists of a cell-wall which encloses a non-nucleated cell protoplasm. The substance of the cell-wall appears in most forms to be composed of cellulose, but in some cases, especially in that of the putrefactive bacteria, it appears to consist of a nitrogenous body in which sulphur and phosphorus are absent, called **myco-protein.**

Microbes may be classified according to their form into the following genera:—

Micrococcus. In this genus (Fig. 149, I) the cells are round or oval in form, colourless, and generally motionless, and about $\frac{1}{5000}$ of a millimetre in diameter. Individual micrococci may live isolated, or large numbers may be bound together in a gelatinous film, called a **zooglœa**, which is probably formed by the conversion of the outer surface of the individual cell-walls into a proteid-containing mucilaginous substance.

Ascococcus in form is similar to *Micrococcus*, but the individuals live in enormous numbers in solid zooglœa colonies of irregular form. It is to be found, together with *Micrococcus*, as wrinkled membranes on the surface of putrefying liquids, the juice of meat, and hay infusion.

Streptococcus (Fig. 149, II) is similar to *Micrococcus*, but it lives in chains, sometimes straight and sometimes curved.

Bacterium. This name, unfortunately, is used both as a generic and as a class name. Used in the generic sense, it is applied to microbes which are short and cylindrical in form (Fig. 149, III), and that may live either as isolated individuals or in zooglœa. Bacterium is not a motionless form, but the individuals are to be seen in a state of vibratory motion, or an undulatory one, always forwards and never backwards; if its forward movement is stopped by a foreign body, it will remain indefinitely undulating before it, never seeming to tire. The motion of

bacteria is due to the presence of a cilium or vibratile protoplasmic filament, either at the hinder end or at both extremities of the cell. The cilium is in very rapid motion and so cannot be seen while the bacterium lives, but needs to be stained by some appropriate stain, such as methyl-violet, in order to render its presence manifest. *Bacterium termo* is a very common form, and is to be found in smaller or larger numbers, in nearly all waters, especially if it has been allowed to stand still for several days exposed to the air, or it can be easily obtained in hay-infusions or putrefying meat juices. Most bacteria, like nearly all other microbes, are colourless and devoid of chlorophyll, but two species (*Bacterium viride* and *B. chlorinum*) are green in colour, due to contained chlorophyll. These bacteria therefore, like green-plants, can under the influence of sunlight utilize the CO_2 of the atmosphere, or of the liquid in which they live, for the purposes of nutrition.

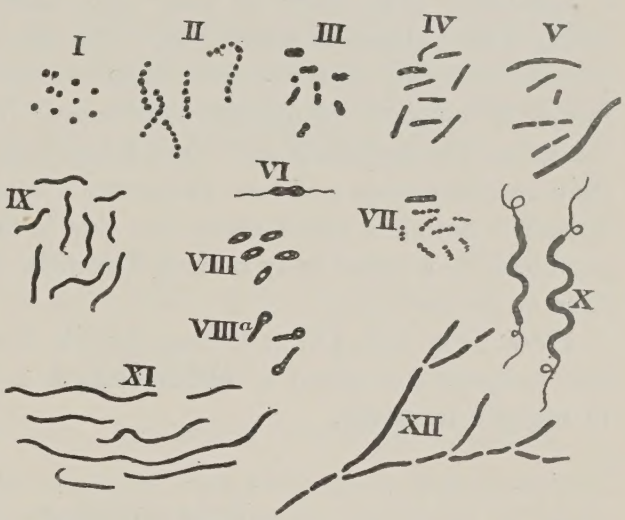


FIG. 149. The forms of Bacteria. I. *Micrococcus*. II. *Streptococcus*. III. *Bacterium termo*. IV. Bacillus of tuberculosis. V. *Bacillus subtilis*, showing stages passing into the *Leptothrix* condition. VI. *Bacterium termo* more highly magnified (2,000 times) than in III. VII. Bacillus of glanders; most of them are dividing and appear to be what at a later stage they really are, i.e. broken up into free spores. This appearance is due to the particular method of staining used, in which the cell-wall is decolourized, only the protoplasm remaining stained. VIII. Spore formation in Bacillus. VIII[a]. Spore formation in Bacillus of tetanus (lock-jaw). IX. *Vibrio*. X. *Spirillum*. XI. *Leptothrix*. XII. *Cladothrix*.

Bacillus. This is a genus characterized by its filamentous form, the filaments being short, flexible, and jointed (Fig. 149, IV and V). It is the genus found in most fermenting liquids, and in the blood or tissues of animals that have died of anthrax and other diseases. In form it is much longer and more obviously filamentous than bacterium, though some bacilli very nearly approach the form of bacterium. Most bacilli are devoid of a cilium and are therefore motionless, though some of them when isolated or in short chains (jointed filaments), like *Bacillus subtilis* and most of the bacilli of putrefaction, possess a cilium at one extremity and are con-

sequently motile. Some species of bacillus (Fig. 149, XI) are capable of dividing repeatedly in a transverse direction into a number of cells, which instead of being set free, remain united end to end, and form a long, unbranched filament; this form is known as *Leptothrix*, and is common in human saliva and putrid substances. *Cladothrix* (Fig. 149, XII) is a long, filamentous form, like *Leptothrix*, but it branches repeatedly in a furcate manner; it is found as a whitish mucilage on the surface of putrefying liquids.

Spirillum (Fig. 149, X) and *Spirochæte* are spiral filamentous forms, with a cilium at either end. The latter is found in the blood of persons suffering from recurrent fever and in stagnant water, and the former in infusions of organic substances. In *Spirochæte* the coils of the spiral are numerous and closely approximated, while in *Spirillum* they are more open and less numerous. When in motion both forms appear to undulate like a worm, but this is due to the optical delusion produced by a spiral body moving forwards and rotating at the same time on its own axis.

Vibrio (Fig. 149, IX) is a long, flexible filament with a wavy form, and possessing a cilium at either end; it is very motile, and is found in organic infusions.

Reproduction.

All bacteria reproduce and multiply by the simple process of transverse fission, which takes place with great rapidity, so that a single bacterium may in the course of a single day give rise to a progeny of many millions, calculated to an approximate degree to be as many as 17,000,000 under favourable conditions. Very frequently the daughter-cells do not separate from one another, but remain connected and form chains. Reproduction by fission may take place while the microbes are in the resting or motile condition.

Bacillus reproduces also by the formation of internal spores. A bright dot (Fig. 149, VIII) appears at one spot in the filament, and this increases in size and becomes oval or round in form, and thus gives rise to an **endospore**, or spore formed within the parent-cell. The endospore is liberated by the rupture of the parent-cell wall, and after a period of rest it germinates under favourable conditions by growing out at one end and thus assuming the form of the parent-cell. The spores, unlike the adult cells, do not stain with aniline dyes; and they are extremely resistant, the spores of some bacteria surviving boiling in water for

over an hour, and many of them resist excessive cold, far below that of the freezing-point of water.

There is good reason to believe that what we regard as distinct genera, i. e. *Bacillus*, *Bacterium*, *Spirillum*, &c., may possibly be but different forms of the same genus varying under varying conditions, i. e. the one form may pass into the other.

With regard to the reaction of bacteria to the air, it is known that some can flourish best in the presence of free oxygen, while others, like that causing the butyric acid fermentation for instance, are paralysed or even killed by the presence of this gas. Hence they may be divided into the **aërobic** forms, or those that require free oxygen for the full display of their activities, and the **anaërobic** forms, or those whose activities are inhibited by free oxygen.

CHAPTER XVI

LICHENS

(A.) The Nature and Different Forms of Lichens.

Having considered the structure and life-history of a number of common fungal and algal types, we are now in a position to briefly consider a group of organisms called the **lichens**, which are of great interest from several points of view.

Much discussion has taken place respecting the systematic position of the lichens since Schwendener in 1868 propounded the 'Schwenderian theory,' as it has been called by its opponents, and sought to prove that all lichens are really **compound organisms**, each form consisting of a fungus and an alga living together. We have, in *Pythium*, already studied a plant which usually lives in the closest connexion with another, even penetrating into its cells, but the advantage of the **parasitic** mode of life in such a case is entirely one-sided, since the host-plant finally yields in the struggle by death. There are, however, very many degrees of parasitism, and in some cases the host appears to suffer but little inconvenience from its connexion with the parasite.

The lichens offer, perhaps, the best example known of plants of quite different habits which, while still retaining their individuality, live together and build up what appears to be one organism, and in which

each individual derives benefit from its association with the other. This condition of mutual help, called **mutualism** or **symbiosis**, in which both organisms 'give and take,' has been shown to exist in many combinations not only of plant with plant, but of plant with animal, and some of these will be mentioned in a later part of this work (pp. 307, 333, 393 and 420).

If the student clearly understands the essential points of difference in the nutrition of fungi and algæ, he will readily understand that a composite organism consisting of green algal cells (known in lichens as **gonidia**) enclosed within a body composed of fungal hyphæ is in a very favourable position with regard to its environment. That this is so is proved by the fact that the composite organism will flourish in situations where neither could live separately. These dry, slow-living, but long-lived plants will flourish at high altitudes and in high latitudes such as no other plants are able to endure. The reason for this is not far to seek. A lichen requires nothing more than a little water with mineral food which it draws up through its rhizoids—everything else it manufactures for itself. The algal cells (like all other cells containing chlorophyll) when exposed to light make organic matter, some of which passes to the fungus and nourishes it; on the other hand, the fungus supplies the alga with water and mineral food, and protects it from desiccation and death in the exposed situations in which lichens can live. The alga may thus live for many years under conditions which would speedily be fatal if it were not protected by the fungus. Indeed, we have in the lichens as good an example as is possible of a division of labour between two originally distinct organisms, to produce a compound one with distinct characters of its own, which yet preserves such an amount of individuality in its constituents as to leave no reasonable doubt of its dual nature. But what is the evidence on which the now almost universal belief in the dual nature of the lichen thallus is based? The earlier botanists took a different view of the matter, and regarded a lichen not as two, but as one organism, and they made a special class of the Thallophyta to include them, considering the class **Lichenes** as equal to either the **Fungi** or the **Algæ**.

The principal evidences on which the dual structure is supported are the following:—

(1) The algal cells which are found within lichens can be referred with certainty to definite genera and species of ordinary algæ, such as *Cystococcus* (a near relative of the *Pleurococcus* found on tree-trunks,

&c.). The algæ are all low unicellular green or blue-green forms comparable with *Hæmatococcus* and *Pleurococcus*.

(2) Even when the algal cells have formed part of a lichen thallus they may be isolated, and are then able to live an independent life.

(3) The fungal portion of the organism consists of interwoven hyphæ just as in ordinary fungal mycelia. The fungus forms reproductive organs known as **apothecia**, containing asci and ascospores, thus showing that the fungus is generally to be referred to the same class to which *Eurotium* belongs, viz. the Ascomycetes.

The fungal part of a lichen can be produced by sowing the spores in a suitable food solution, but unless algal cells are also introduced it never forms gonidia.

(4) The most conclusive evidence is afforded by the fact that some lichens have been formed *synthetically* by sowing spores of the fungus among the appropriate algal cells. When the spores germinate they form the usual fungal hyphæ : these branch and clasp the algal cells, and the two together gradually build up a lichen thallus. The fungal hyphae do not actually penetrate the algal cells, as is commonly the case in parasitism, but they come into such intimate contact that we are justified in believing an interchange of food material is readily effected.

Lichens commonly live on walls and roofs, rocks, the bark of trees, sometimes on the ground, and in other exposed situations. They exhibit considerable variation in their mode of growth, consistency, &c., and may be roughly divided into the following four main divisions :—

(1) **Fruticose Lichens**, which grow erect and branch in a shrub-like manner. Some of these forms are very common on trees.

(2) **Foliaceous Lichens.** In these the thallus is more or less flattened with a lobed margin, and is attached to the substratum by rhizoids. A common example is *Parmelia* (*Physcia*), the orange-coloured thallus of which is familiar on roofs, &c.

(3) **Crustaceous Lichens.** These are found closely adhering to rocks, walls, trees, &c., and are often so hard, thin, and indefinite in outline that they can scarcely be distinguished from the material on which they are growing.

In all three of the above divisions the gonidial cells are arranged in a definite layer (**gonidial layer**) near to the upper surface of the thallus, as in *Parmelia* (Fig. 150).

(4) **Gelatinous Lichens.** Soft forms consisting of fungal hyphæ

and gonidia embedded in a mucilaginous matrix. Ex. *Collema.* In this division the gonidial cells are scattered throughout the thallus.

The lichens are now generally classified with the fungi on account of their fungal mode of reproduction.

PARMELIA (PHYSCIA) PARIETINA.

Our type is a very common lichen, well known by its orange colour, and, as already mentioned, is a foliaceous form. Its flattened thallus (Fig. 150, I) is attached by the greater part of its lower surface to the substance on which it grows by a large number of **rhizoids,** which are really only free fungal hyphæ that perform the functions of roots in attaching the plant and in the absorption of water which falls on the roof or wall to which the plant is attached.

The growing edge of the thallus, which is not attached to the substratum, generally has a more or less crinkled appearance. Scattered over the upper surface of the thallus, a number, often a large number, of very shallow cup-like structures (A) are seen. These are of varying sizes, the largest (oldest) being near the centre or oldest portion of the thallus, while those near the growing edge are young and consequently small. These cups are reproductive organs known as **apothecia,** and they consist, like the fructification of all lichens, of the fungal constituent only, and therefore contain no green cells.

(B.) Structure of Thallus.

If we cut a transverse (vertical) section of the thallus of *Parmelia* and examine it with a high power, it will be seen that the upper portion (Fig. 150, II, UC), which is known as the **upper cortical layer,** is composed of a parenchymatous-looking tissue, but in reality consists of hyphæ which are here closely packed and interwoven so that there are no interspaces. A similar cortical layer (LC) constitutes the lower portion of the thallus, while between the two is a **medullary zone** (M) in which the hyphæ are loosely arranged, and with large air-spaces between them. Just below the upper cortical layer, and occupying some of the spaces in the medullary zone, are the algal cells or **gonidia** (G), which have been proved in this case to be a species of *Cystococcus*, one of the lower green algæ closely related to the *Pleurococcus* found on tree-trunks, damp palings, &c.

(C.) Reproductive Organs and Reproduction.

The algal cells (**gonidia**) take no part in the production of the *special* reproductive cells formed by lichens, although they form a part of the **soredia** mentioned below. The gonidia, however, divide vegetatively so as to keep pace with the increasing size of the thallus; this division is a simple one into two, four, &c., and is strictly comparable to the similar division of *Pleurococcus* and other free algal cells.

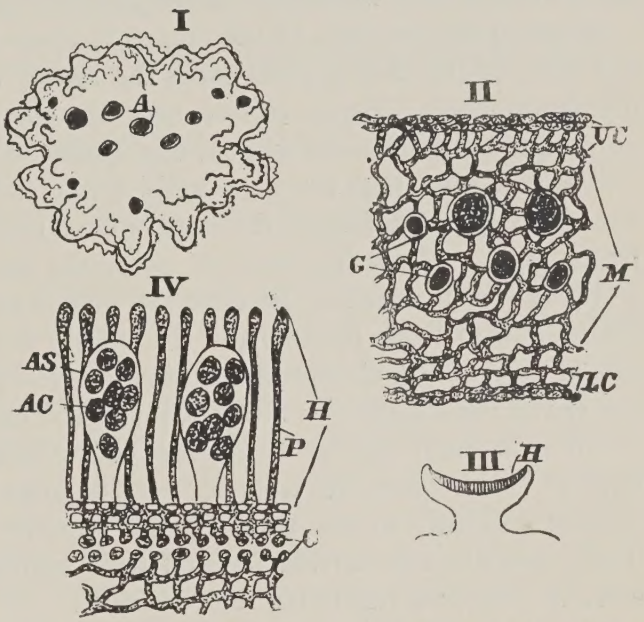


Fig. 150. *Parmelia parietina.* I. Upper surface-view of thallus. Enlarged one and a half times. II. Transverse section of thallus. Magnified 300 times. III. Vertical section of an apothecium. Magnified 20 times. IV. Portion of a vertical section of an apothecium. Magnified 300 times. A= apothecium; AC=ascospore; AS=ascus; G=gonidia; H= hymenium; LC=lower cortical layer; M=medullary zone; P=paraphysis; UC=upper cortical layer.

The fungus, however, forms special reproductive organs, viz., the **apothecia** (Fig. 150, I, A, and III) before mentioned, but these do not differ in any important points of structure from the fructifications formed by ordinary ascomycetous fungi living a separate existence. Each apothecium is really a shallow cup supported on a very short stalk. Within the slightly elevated rim of an apothecium the surface is formed by a spore-bearing layer known as the **hymenium** (cp. *Agaricus*, p. 258). A vertical section through an apothecium (III and IV) shows that the hymenium (H) itself consists of two kinds of elements, i.e. the peculiar kind of sporangia known as **asci** (AS) (see *Eurotium*, p. 265), each containing eight **ascospores** (AC), and of smaller sterile hairs known as **paraphyses** (P). The apothecia continue to grow outwards from the edges for a long time and to form fresh asci and spores as they do so. When ripe the asci expel their spores, which are, however, only capable of forming new lichen thalli if the

necessary *Cystococcus* cells are present where the spores germinate. There is yet some doubt as to whether the apothecia are concerned in reproduction by a sexual act or not. Small flask-shaped cavities known as **spermogonia** are formed in the thallus, and in the walls of these arise long filaments from which very small cells known as **spermatia** are budded off. It has been supposed that the spermatia are really male cells which are conveyed by water to the female organ from which asci subsequently grow.

A sexual act appears to take place in some lichens (e. g. *Collema*), but it is possible that in most cases the sexual organs, though present, are functionless. However this may be, the spermatia are able to germinate by themselves without conjugation with other cells.

We have seen that the algal cells divide and so give rise to fresh ones, and that the fungus develops spores capable of forming fungal hyphæ only. *Parmelia*, however, possesses one mode of reproduction which is very interesting, because the bodies produced are capable of giving rise to fresh lichens, and not merely to either the algal or the fungal portion. A change takes place in the gonidial layer whereby the tissue breaks up into little groups called **soredia**, each consisting of one or a small number of gonidial cells closely invested with fungal hyphæ. Ultimately the isolated soredia form a powdery mass and become exposed to the wind by the rupture of the upper cortex. These soredia are carried far and wide through the air and afford a ready means of vegetative reproduction.

PART II

SPECIAL MORPHOLOGY AND CLASSIFICATION OF ANGIOSPERMS

CHAPTER XVII

THE FLOWER AND INFLORESCENCE

THE flowers of the angiosperms, the so-called 'flowering plants,' are morphologically leafy shoots, some or all of the leaves of which have undergone modification into spore-bearing leaves or *sporophylls*, the spores in this case being commonly known as pollen grains (*microspores*) and embryo-sacs (*macrospores*) (see Part I, pp. 128 and 132). It will be at once seen that this definition of a flower as a reproductive shoot applies equally to the male and female cones of *Pinus* (which are therefore correctly described as 'flowers') as well as to the spike of *Selaginella*, which also consists of an axis bearing leaves (sporophylls) and sporangia with spores.

The comparison may even be carried as far down in the scale of vegetable life as the mosses ; the male plant of *Polytrichum*, for instance, has its apical antheridia surrounded by a kind of perianth formed of a rosette of reddish leaves, the whole having a striking resemblance to a flower (Part I, p. 216). In this case, however, it should be noticed that the apparent flower belongs to the gametophyte generation, and not to the sporophyte generation to which the 'flowers' of *Selaginella*, *Pinus*, and the Angiosperm belong.

But although the spikes of *Selaginella* and the cones of *Pinus* are to be regarded strictly as flowers in the technical sense, it is patent to every one that these are not the structures to which the name 'flower' is commonly applied, and that the flowers of the angiosperms have usually certain special characters of their own. The cryptogamic and gymnospermic flowers above mentioned show clearly the elongation of the internodes and consequent separation of the sporophylls

to which the distinctive character of the *cone* or *spike*[1] is due; in the angiosperm this elongation of the internodes does not take place (or only in exceptional cases), and so the more or less modified leaves or whorls of leaves which constitute the flower arise at nearly the same level on the axis.

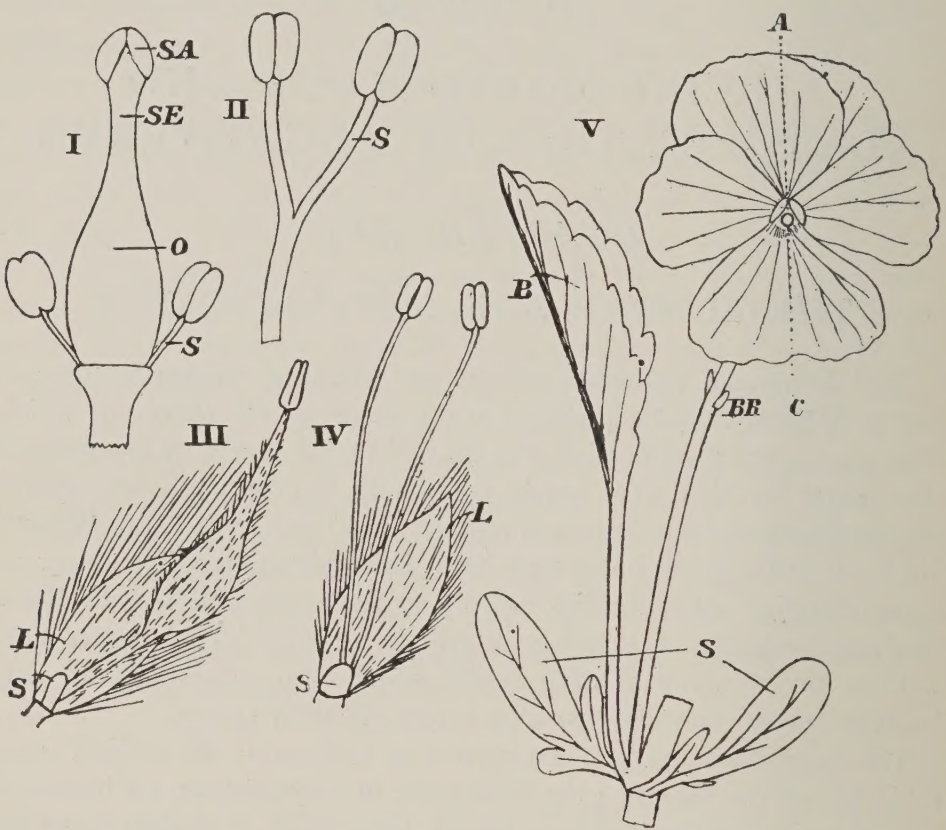


FIG. 151. I. Hermaphrodite achlamydeous flower of the Ash with two stamens (S) and bicarpellary ovary (O). SA=stigma; SE=style. II. Male flower of the Ash with two stamens only. III. Scale (L) from the female catkin of the Willow with a bicarpellary pistil in its axil. S=nectary. IV. Scale (L) from a male catkin of the Willow with two stamens and nectary (S). V. Pansy (*Viola tricolor*), showing flower in the axil of a bract (B) with two large leafy stipules (S). The flower-stalk or pedicel bears two bracteoles (BR) (these should be nearer to the flower). The flower is medianly zygomorphic, its plane of symmetry being along AC. The bracts are ordinary foliage leaves, and the flowers are solitary and axillary.

Perhaps the most distinctive feature of the angiospermic flower is the general association with the sporophylls of a number of more or less modified leaves forming a perianth, some or all of the members of which may be large and brightly coloured to serve as an attraction

[1] The term 'spike' is not here used in the same sense as that applied to inflorescences (supra, p. 300).

to insects. A perianth is, however, very frequently absent even in angiosperms, as for example in the male and female flowers of the willow, the ash, &c. (Fig. 151), while, although the flowers of *Pinus* have no perianth, those of the highest gymnosperms (the *Gnetaceæ*) have.

In most cases the flower includes both stamens (*microsporophylls*) and carpels (*macrosporophylls*), and is therefore described as **hermaphrodite**, but frequently one or other of these sets of organs is absent and the flower becomes in consequence **unisexual**, either **staminate** (male) or **carpellary** (pistillate or female) (Fig. 151). The unisexual condition is characteristic of the flowers of certain natural orders (*Cucurbitaceæ*, *Salicaceæ*, &c.), but it may also be developed in certain plants belonging to orders which are typically hermaphrodite. There is reason to believe that in some cases (e.g. the willow and the oak) the unisexual condition is the primitive one and is not the result of abortion of parts in the development of the flower, but in others (e.g. the red campion among *Caryophyllaceæ* and the sorrels among *Polygonaceæ*) the presence of rudimentary organs, such as staminodia or rudimentary stamens, or indications of such in development, and comparison with closely-allied forms, leads to the conclusion that suppression of either stamens or carpels has taken place and the unisexual condition is therefore not the primitive one, but has been secondarily acquired in the course of evolution.

When the flowers are unisexual the male and female flowers may be either borne on the same plant or on distinct individuals; in the latter case we have not only distinct male and female *flowers*, but also *distinct male and female plants*. In the former case the plant is described as **monœcious**, as in the birch (*Betula*), alder (*Alnus*), oak (*Quercus*), beech (*Fagus*), hazel (*Corylus*), *Arum*, box (*Buxus*), &c.; when there are distinct male and female individuals the plant is **dicœcious**, as in the willow (*Salix*), poplar (*Populus*), white bryony (*Bryonia*, Fig. 185), red and white campions (*Lychnis*), &c.

A plant may also bear both hermaphrodite and unisexual flowers. This **polygamous** condition is found in the common ash (*Fraxinus excelsior*), which commonly bears hermaphrodite flowers, and others in which only the two stamens are present (Fig. 151, I and II).

As already mentioned, it is characteristic of the angiospermic flower that the internodes between the floral leaves (sporophylls, and, if present, perianth leaves also) remain undeveloped; to this shortened axis, which is commonly expanded, and either flat, convex (e.g. butter-

cup, Fig. 178), or concave (e.g. rose, Fig. 183), the term **receptacle** or **torus** is applied. If a more or less elongated axis or stalk is present below the flower it is described as the **pedicel** of the flower, and the axis from which it arises (unless it be a terminal flower) the mother axis. If no pedicel is present and the flower is situated directly on the mother axis it is **sessile**, as in *Compositæ* (see sunflower, p. 24).

The flower itself (whether pedicellate or sessile) commonly arises, just as an ordinary vegetative shoot does, in the axil of a leaf (the **bract**), which may be quite like one of the ordinary foliage leaves of

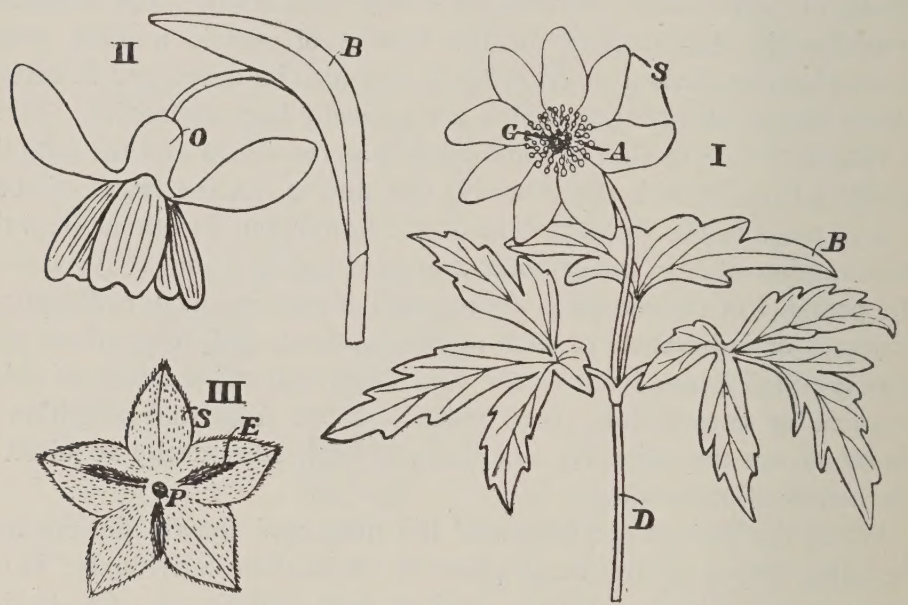


FIG. 152. I. Wood Anemone, showing the whorl of three large leafy bracteoles (B) borne on the peduncle (D) below the flower. A=indefinite stamens; G=numerous carpels; S=petaloid (white) sepals. The flower is solitary and terminal. II. Snowdrop flower, showing the sheathing bract or spathe (B). O=inferior ovary. III. Flower of Mallow from below, showing the calyx (S) and epicalyx (E). P=cut pedicel. The epicalyx consists of three bracteoles.

the plant (e.g. pansy, Fig. 151), but is commonly more or less modified in size, texture, or colour. The foregoing is to be considered as the strict definition of a bract, i.e., a leaf in the axil of which a flower arises, but it is usual to use the term also in a wider and more general sense to include all leaves (other than sporophylls and perianth leaves) which are closely associated with the flowers. In this wider sense the **spathe** of many monocotyledons (e.g. *Arum*, *Richardia*, palms, *Narcissus*, snowflake, &c.) and the involucral leaves of *Compositæ*, &c., may be regarded as bracts, although they surround in most cases whole inflorescences and not single flowers.

The small leaves commonly borne on the pedicel itself below the flower are described as **bracteoles** or **prophylla**; of these there is usually one in monocotyledons and two in dicotyledons (Fig. 151, V). In some cases, as in the anemones (*Ranunculaceæ*), the large leafy bracteoles are arranged in a whorl of three, either quite close to the flower and thereby simulating a calyx, as in the hepatica (*Anemone Hepatica*), or at some distance below the flower, as in the common wood anemone (*A. Nemorosa*, Fig. 152, I). The **epicalyx** of the mallow (*Malva*, Fig. 151, III), hollyhock (*Althæa*), &c., is also of this nature; while that of *Potentilla*, *Geum*, and other *Rosaceæ*, consists, not of bracteoles, but of stipular (supra, p. 10) appendages to the calyx leaves.

The Arrangement of the Parts of the Flower on the Receptacle, and their Numerical Relationships.

The floral leaves (*sepals*, *petals*, *stamens*, *carpels*) are commonly arranged in *whorls*, each series occupying one or more whorls as the case may be; when this is the case the flower is described as **cyclic**. Sometimes, however, some or all of the floral leaves are developed successively and in a *spiral*, as in so many foliage leaves; in such cases the flowers are described as **acyclic** when all the floral leaves are spirally arranged, or **hemicyclic** when some only are spiral and the others whorled. The white water-lily (*Nymphæa*) shows a common result of the acyclic arrangement, viz. the absence of definite distinction of the several series, sepals passing into petals and petals into stamens by a number of intermediate forms.

Several conditions are possible in hemicyclic flowers; some or all of the perianth leaves may be cyclic, while the stamens and carpels are spirally arranged (e.g. *Ranunculus*), or the perianth leaves may be spiral and the sporophylls cylic. In a large number of dicotyledonous natural orders the five sepals are spirally arranged and occupy two turns of the spiral.

In what may be described as a typical angiospermous flower there are four series of more or less modified floral leaves which are named as follows, starting from without (or below):—(1) the sepals together constituting the *calyx*; (2) the petals forming the *corolla*; (3) the stamens the *andrœcium*; and (4) the carpels the *gynœcium*. If a flower is devoid of a perianth, as in the willow, arum, &c., it is **naked** or **achlamydeous** (Fig. 151, I–IV); if a perianth is present the

flower is either **monochlamydeous** or **dichlamydeous**, according as one or both series (calyx and corolla) are present. The dichlamydeous condition is usual, but several orders are typically monochlamydeous or achlamydeous (and are accordingly classified as *Incompletæ*), such as the *Urticaceæ* (including the stinging-nettles, hop, elm, &c.), the *Cupuliferæ* (birch, alder, oak, beech, hazel, &c.), the *Salicaceæ* (willows and poplars), *Polygonaceæ*, &c. In certain typically dichlamydeous orders the monochlamydeous condition of certain genera is due to suppression, as in some *Compositæ* (e.g. the daisy) and *Umbelliferæ* in which the calyx is absent; in some *Rosaceæ* (e. g. *Alchemilla* and the burnet) and *Ranunculaceæ* (e.g. *Anemone*, *Clematis*, *Caltha*, &c.) the corolla is suppressed.

The number of whorls of floral leaves in the flower is variable: there may be as few as one (e.g. the naked male flower of the ash) or a great number, as in the rose or columbine, where the stamens form numerous whorls (Fig. 178, IX, p. 357). Typically the flower consists of *four* whorls, one each to the calyx, corolla, andrœcium, and gynæcium, but frequently the number of whorls is increased; the calyx is **polycyclic** (i.e. consists of more than one whorl) in the *Cruciferæ* where it consists of two whorls of two members each; the andrœcium consists of two whorls in many *Caryophyllaceæ* and *Geraniaceæ*, in *Fumariaceæ*, *Cruciferæ*, and in very many monocotyledons (*Liliaceæ*, *Juncaceæ*, *Amaryllidaceæ*, &c.); the gynæcium is but rarely polycyclic, although when it is acyclic (as in many *Ranunculaceæ*) the carpels may occupy several turns of the spiral. The corolla is polycyclic in the *Berberidaceæ* (Fig. 179), *Papaveraceæ*, *Fumariaceæ*, &c., and commonly becomes so in the 'doubling' of flowers by which new whorls of petals are produced at the expense of the essential organs of the flower (i.e. the stamens and carpels).

The number of more or less distinct parts or members in each whorl is also variable. The typical number in dicotyledonous flowers is *five* (e. g. geranium), sometimes *four* (e.g. holly), or *two* (enchanter's nightshade), rarely *three* (e.g. dock); in monocotyledons the number is generally *three*

In the foregoing examples of **pentamerous**, **tetramerous**, or **trimerous** flowers (i.e. with five, four, or three members in a whorl respectively), the number of members in the whorl is constant throughout the flower, i.e. in the geranium there is a calyx of five sepals, a corolla of five petals, two whorls of stamens of five each, and a gynæcium of five carpels. This regularity in number is however

very commonly departed from, especially in the androecium and gynæcium; in most *Labiatæ* and *Scrophulariaceæ*, for instance, the stamens are reduced from five to four and the carpels to two by suppression of parts; in other cases the number of members in a whorl is above the typical number, as in the flowers of the *Cruciferæ*, in which the petals and inner whorl of stamens consist of four members each instead of two as in the sepals, outer whorl of stamens, and carpels.

The members of successive whorls, when they are of the same number, commonly alternate with one another, the petals alternating with the sepals, the stamens with the petals, and so on; sometimes, however, this arrangement is departed from and the members of a whorl are directly superposed on those of the whorl lying immediately outside. This latter condition may be the result of the suppression of an intermediate whorl, as is believed to be the case in the *Primulaceæ*, where the five stamens are directly opposite to the petals (**antipetalous**), instead of being opposite to the sepals (**antisepalous**), as is usual with a monocyclic androecium.

In some few cases one or more of the internodes between the floral leaves is developed, leading to separation of the whorls; thus in some *Caryophyllaceæ* the internode between the calyx and corolla is elongated, constituting an **anthophore**; in the passion-flower a **gonophore** is developed between the corolla and the androecium. The axis of the flower does not grow except as a rare variation above the highest floral leaves.

Hypogynous, Perigynous, and Epigynous Flowers (Fig. 153).

The parts of the flower are developed as a rule in acropetal succession, the calyx first and gynæcium last. If the growth of the axis is entirely apical, the last-formed whorl, that of the carpels, will occupy the highest position, as in the *Ranunculaceæ* (Fig. 178, p. 357), *Cruciferæ*, *Caryophyllaceæ*, &c., the stamens, petals, and sepals being inserted on the axis at successively lower levels. Such a flower is described as **hypogynous**, the same term being applied to the stamens and petals, while the calyx is described as **inferior** and the ovary **superior**. If the growth of the axis is not entirely terminal (apical), but a certain amount of intercalary growth (growth that is not apical) takes place below, or, in a more or less flattened receptacle, around,

the apex, a circular rim will be formed carrying the sepals, petals, and stamens outward and commonly upward to a higher level than the gynæcium. Such a mode of growth, which is characteristic of a number of natural orders, gives rise to **perigynous** flowers. The *Rosaceæ* (see Fig. 183, p. 372) affords an interesting series illustrating different degrees of perigyny; the flowers of the dewberry, blackberry, strawberry, potentilla, &c., should be carefully compared with that of the buttercup, when it will be at once seen that, in the rosaceous flowers mentioned, the stamens, petals, and sepals have been carried outward by intercalary growth, which has evidently taken place at some distance below the apex of the axis; in the cherry and rose the same process has gone on to a much greater extent, resulting in the development of a deep cup (**receptacular cup**, sometimes erroneously described as the calyx-tube), on the floor or sides of which the carpel or carpels are developed, while the other parts of the flower spring from the margin of the cup at a much higher level. In the rose, the opening at the top of the receptacular cup is small, only allowing of the passage of the numerous free styles (see Fig. 183, p. 372). In the apple or pear the arrangement is less easy to make out; the receptacular cup is again nearly closed in at the top; the five free styles indicate the number of carpels, which in this case are partially embedded in the tissue of the receptacle, as will be seen by cutting sections through the receptacle.

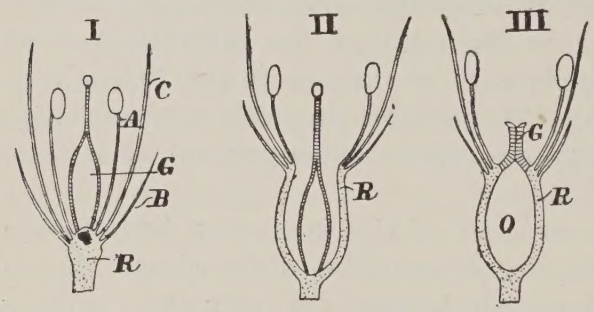


FIG. 153. I. Diagram of a hypogynous flower. A = stamens; B = sepals; C = petals; G = gynæcium; R = receptacle. II. Diagram of a perigynous flower. R = cup-shaped receptacle. III. Diagram of an epigynous flower. O = cavity of the ovary, the wall of which mainly consists of the receptacular tube, and not of the carpels; R = cup-shaped receptacle closed in at the top by the carpels (G).

In some natural orders (*Umbelliferæ*, *Compositæ*, *Cucurbitaceæ*, &c.) the cavity of the ovary (not the cavity in which the ovaries are contained, as in the *Rosaceæ*) is merely a receptacular tube or cup, from the upper rim of which not only the sepals, petals, and stamens, but the carpels themselves are developed, the latter simply serving to close in the ovary at the top. Such a flower is described as **epigynous**, a term which is also applied to the androecium and corolla

separately, the calyx being now **superior** and the ovary **inferior** (Fig. 153, III).

Cohesion and Adhesion of the Parts of the Flower.

The members of a single whorl or of different whorls may develop and remain distinct from one another, as in the buttercup, where each leaf (whether sepal, petal, stamen, or carpel) arises individually from the receptacle, and may be separated without tearing or cutting anything more than its own attachment. The buttercup is a plant in which there is entire absence of both **cohesion** (or union among the members of a single whorl) and **adhesion** (or union of the members of different whorls).

But cohesion and adhesion between some or other of the floral leaves is extremely common, sometimes taking place to such an extent as to cause difficulty in the determination of the number of members in a whorl, or of the number of whorls. Generally, however, some indication of the number of the members is afforded by the number of lobes or points of the perianth leaves, by the free filaments or anthers of the stamens, by the number of styles or stigmas, or by the number of chambers in the ovary.

If the sepals remain free from one another, the calyx is described as **polysepalous** ; if they are more or less coherent, so that their number is indicated only by the number of teeth or lobes springing from the margin of a calyx tube, it is **gamosepalous**. The corresponding terms, **polypetalous** and **gamopetalous**, are applied to the corolla.

In those cases in which the perianth is not clearly differentiated by texture, form, or colour into two series (calyx and corolla), although there are two whorls, as in many monocotyledons, and in plants in which the perianth is really simple (i.e. consists of a single whorl), the terms **polyphyllous** and **gamophyllous** are employed. In those cases in which the apparently simple condition of the perianth is really the result of *suppression* (as is seen in development or by comparison with allied forms), the part of the perianth which is developed should be described as a calyx or corolla, as the case may be ; e.g., the petal-like (**petaloid**) leaves of the flowers of *Clematis*, *Anemone*, *Caltha*, &c., are really sepals, and should be described as such, while in those *Compositæ* in which the calyx is entirely suppressed the remaining whorl is described as a corolla and not as a simple perianth.

In some cases the two whorls of the perianth adhere so as to form a single tube, as in the hyacinth.

The stamens may cohere with one another, or they may adhere to the corolla or perianth, or even, rarely, to the gynæcium. The cohesion may be between the lower portions of the filaments only, while the anthers remain free, as in the *Leguminosæ*, some *Geraniaceæ*, *Malvaceæ*, and *Hypericaceæ* (Fig. 154); in the two latter orders the filaments are also branched. When the filaments are all coherent

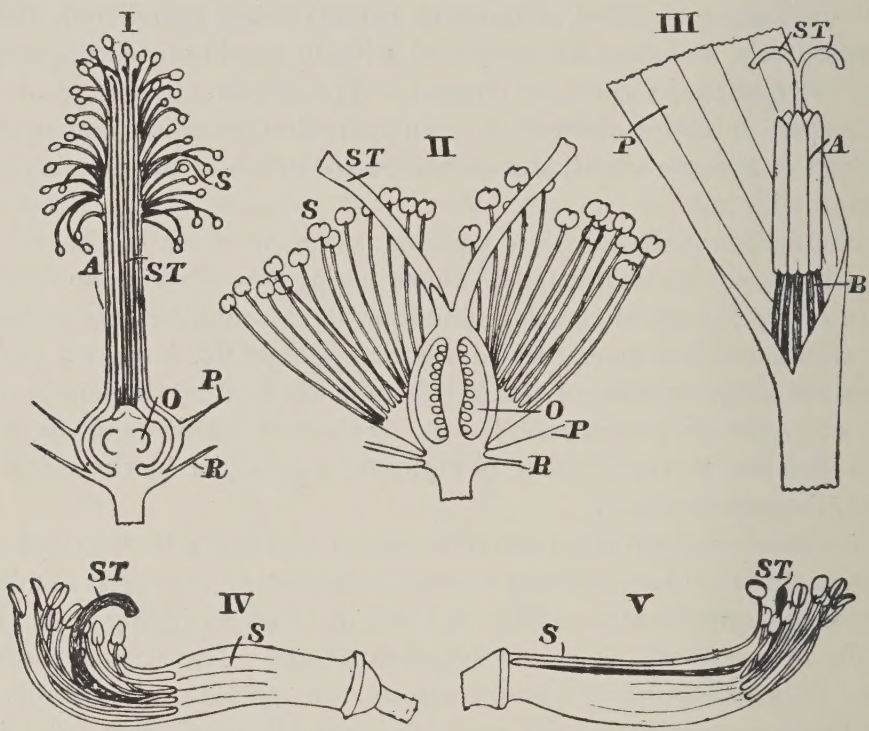


FIG. 154. 1. Vertical section of the central part of the flower of Mallow (*Malva*). A = staminal tube; O = ovary; P = corolla adnate to the base of the staminal tube; R = calyx; S = stamens; ST = free styles in staminal tube. II. Vertical section showing the central organs of the flower of St. John's Wort (*Hypericum*). Letters as in I. Two bundles of stamens are shown, and two of the free styles. The placentation in the ovary (O) is axile. III. Part of a flower of one of the *Compositæ*. A = syngenesious anthers; B = free filaments; P = part of the ligulate corolla; ST = the two stigmas. IV. Monadelphous androecium of the Broom (*Cytisus*). S = tube formed of the coherent filaments of the stamens; ST = style and stigma. V. Diadelphous androecium of the Pea (*Pisum*). S = the single free stamen; ST = stigma.

into a single bundle, as in the *Malvaceæ* and many *Leguminosæ*, the stamens are described as **monadelphous**, when in two bundles (e.g. other *Leguminosæ* and *Fumariaceæ*) **diadelphous**, or in several bundles, as in *Hypericum*, **polyadelphous** (Fig. 154, II). Sometimes the cohesion takes place by the anthers, while the filaments remain free, as in the *Compositæ*, potato (*Solanum*), &c., in which the anthers are described as **syngenesious** (Fig. 154, III). When the stamens are

adherent to the corolla or to the perianth, i.e. *when both whorls are raised on a common tube*, the stamens are described as **epipetalous** or **epiphyllous**, a condition which is very commonly found in those orders in which the corolla is gamopetalous. Adhesion of the stamen or stamens to the carpels is rare, but is found in *Orchidaceæ*, the flowers of which are described in consequence as **gynandrous** (see p. 353).

Lastly, the carpels may exhibit more or less complete fusion with one another. In those cases in which no cohesion takes place, each carpellary leaf simply closing by its edges and forming a separate ovary, the pistil is described as **apocarpous**, as in most *Ranunculaceæ* (Fig. 178, p. 357), *Rosaceæ*, *Crassulaceæ* (Fig. 155, I), *Alismaceæ*, *Butomaceæ*, &c. In those plants in which only a single carpel is present (e.g. the cherry and many other *Rosaceæ*, *Leguminosæ*, *Berberis*, &c.), the gynæcium is described as apocarpous and simple (Figs. 155, IV, and 179). When cohesion takes place between the carpels in a multicarpellary gynæcium, the latter becomes more or less completely **syncarpous**. The extent of this fusion is subject to considerable variation in different plants; in the saxifrage the carpels cohere only by their lower ends, the upper parts of the ovaries and the styles and stigmas being free (Fig. 155, II); the carpels may cohere to form a single ovary, while the styles and stigmas remain separate, as in the *Caryophyllaceæ* (Fig. 181, III, p. 365); only the ends of the styles or stigmas may be free, as in *Compositæ* (Fig. 154, III); or the stigmas may even fuse into a knob (**capitate stigma**), as in the primrose (Fig. 155, III).

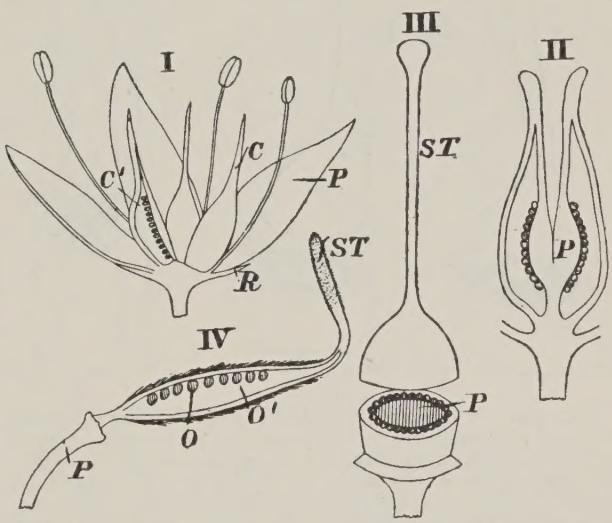


FIG. 155. I. Vertical section of a flower of *Crassula*. C=one of the free carpels; C'=carpel cut open, showing the ovules arranged along the ventral suture; P=corolla; R=calyx. Pistil apocarpous; placentation marginal. II. Vertical section of the gynæcium of a Saxifrage, showing the cohesion of the carpels at the base. P=the placentas. Placentation axile. III. Gynæcium of the Primrose. P=central placenta; ST=style terminated by the capitate stigma at the top. Placentation free central. IV. Gynæcium of the Sweet Pea. O=ovules; O'=cavity of the single carpel; P=pedicel; ST=style and stigma. Placentation marginal.

The cohesion of the carpellary leaves to form a single syncarpous ovary may take place in several ways; they may merely cohere by their edges, as in the *Violaceæ* (Fig. 156, I), to form a syncarpous but **unilocular ovary**; or outgrowths may take place from the margins (**ventral sutures**) of the carpellary leaves to form placentas which project into the cavity of the ovary but do not meet in the centre, as in the poppy, where the ovary is still unilocular (Fig. 168, II, p. 321); when, as in the tulip (Fig. 156, III) and in a large number of other plants, the ovary originates from the growing-point of the flower as a number of coherent tubes with the ovules attached to their inner margins, it becomes **multilocular**, and is described as *bi-*, *tri-*, *pentalocular*, according to the number of loculi formed. In epigynous flowers (e.g. *Amaryllidaceæ*), where the wall of the ovary is not formed by the carpels but by the receptacle, the septa of the ovary are formed by downgrowth of the margins of the carpels along the internal surface of the cavity.

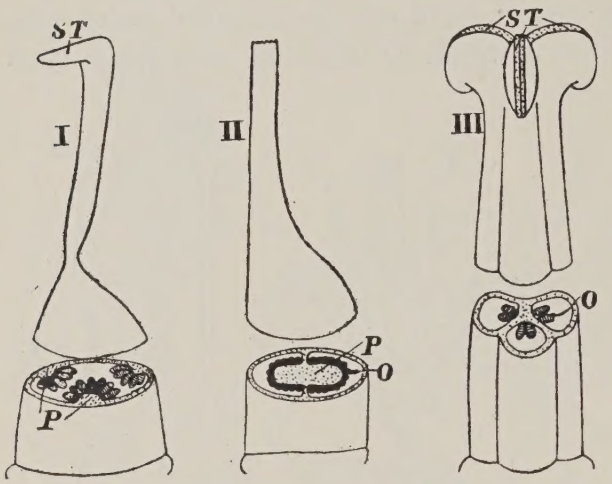


FIG. 156. I. Gynæcium of the Violet, showing the three parietal placentas (P) in the ovary. ST=stigma. Ovary syncarpous but unilocular. II. Gynæcium of the Foxglove. The upper part of the style has been cut off. O=ovules; P=placentas. Ovary syncarpous and bilocular; placentation axile. III. Gynæcium of the Tulip. O=ovules; ST=stigmas. Ovary syncarpous and trilocular; placentation axile.

In some cases the axis is prolonged between the carpels, forming a **carpophore**, from which the carpels afterwards separate, as in the *Umbelliferæ* and *Geraniaceæ* (Fig. 182, III, p. 369).

Floral Diagrams and Formulæ.

A convenient way of indicating the number and relations of the floral leaves is by means of **floral diagrams**. In such a diagram of a cyclic flower, the sepals, petals, &c. are indicated as lying on a number of concentric circles, of which the outer are occupied by the sepals (if present), and the inner by the carpels as being the uppermost

series of organs, even in epigynous flowers. It is convenient to adopt symbols which recall certain peculiarities of the organs indicated; thus the stamens are represented by diagrammatic transverse sections of the anthers, the sepals are distinguished from petals by the indication of a midrib in the former, &c. Many special characters may

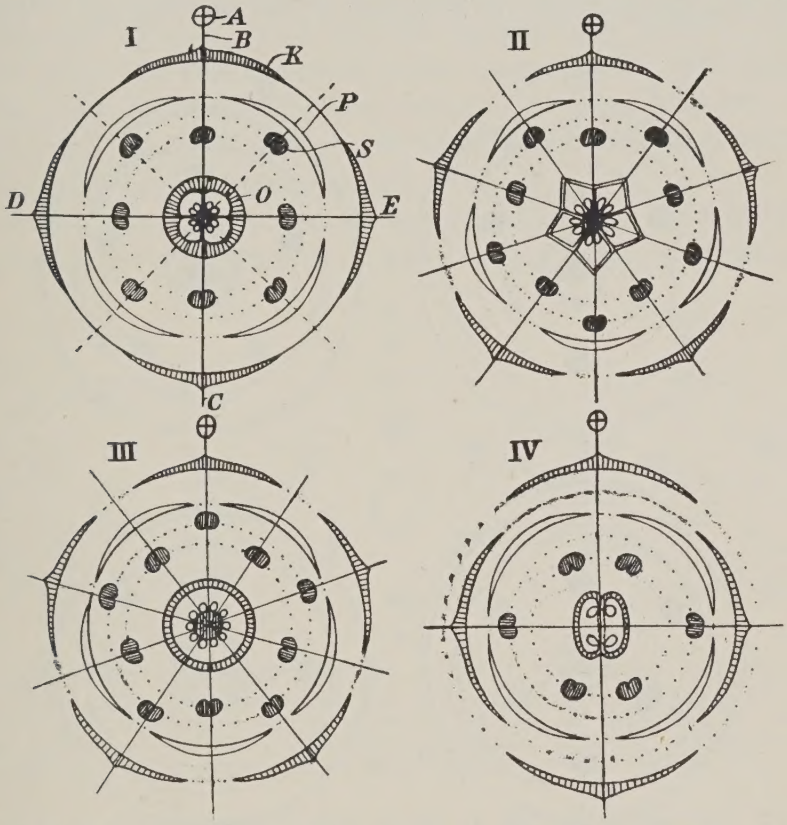


FIG. 157. Floral diagrams. I. Floral diagram of most *Onagraceæ*. A=main axis on which the flower is borne; BC=median or antero-posterior plane, B is posterior and C anterior; DE=lateral plane. The dotted lines indicate the diagonal planes. K=sepals; O=four-celled ovary. Traces of four planes of symmetry are shown. P=petals; S=obdiplostemonous stamens. II. Floral diagram of Geranium. Flower pentamerous. Stamens obdiplostemonous. Five planes of symmetry. III. Floral diagram of most *Caryophyllaceæ*. Flower pentamerous. Five planes of symmetry. IV. Floral diagram of *Cruciferæ*. Sepals and stamens in two whorls. Outer stamens and carpels lateral. Traces of two planes of symmetry are shown, but the halves produced by section along one plane are unlike those produced in the other. Symmetry isobilateral.

also be indicated in a floral diagram, such as cohesion and adhesion, the former by lines connecting the members of the same whorl, the latter those of different whorls (Fig. 188, VII, p. 391). When there is no cohesion, the circles on which the diagram is constructed may be dotted in (Fig. 178, IX, p. 357). Anthers which dehisce outwards (**extrorse**) instead of inwards (**introrse**) may be indicated by drawing

the anther-symbols the other way about (Fig. 158, I). Spurs, glands, &c. may be indicated; as may also the arrangement of the ovules in the ovary (**placentation**).

If the flower indicated is not a terminal one, the position of the main axis (i. e. the axis on which the flower is borne) should be indicated by a dot or small circle placed above the diagram. The bract

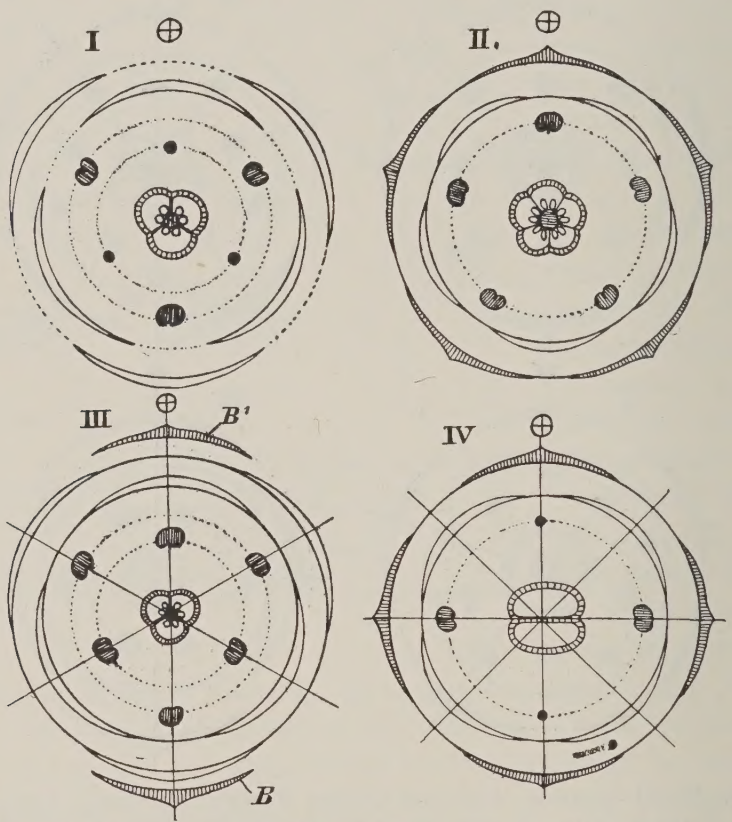


FIG. 158. Floral diagrams. I. *Iris*. All the members of the dicyclic perianth are represented alike. Anthers extrorse. Inner whorl of stamens suppressed. Ovary trilocular; placentation axile. II. *Campanula*. Flower regularly pentamerous. III. Lily. B=bract; B′=posterior bracteole. The typical arrangement in monocotyledons. Traces of three planes of symmetry are shown. IV. Floral diagram of many *Oleaceæ*. Flower tetramerous. Anterior and posterior stamens suppressed. Carpels median.

(if present) may be also indicated, and will lie below the diagram; the bracteole or bracteoles may also be shown (Fig. 158, III).

The side of the flower towards the main axis is **posterior**, that towards the bract or away from the main axis, **anterior**. If a line is drawn as in Fig. 157, I, passing through the main axis and the centre of the flower, it indicates the **median** or **antero-posterior plane** of the flower; one at right angles to this, but also passing through the centre

of the flower, indicates the **lateral plane**, while planes which bisect the angles formed by the median and lateral planes are known as the **diagonal planes**; all other planes are said to be **oblique**. Thus in the *Oleaceæ* (Fig. 158, IV) the sepals of the tetramerous calyx lie two in the median and two in the lateral planes; the petals lie in the diagonal planes; the two stamens are lateral (the median ones, being suppressed, are indicated by dots), and the two carpels are median. In the *Liliaceæ* (Fig. 158, III) one sepal (often known as the **odd sepal**) is anterior, as is also one of the outer whorl of stamens and one of the carpels; the odd petal and one of the inner whorl of stamens are posterior; all the other members are oblique.

Floral diagrams are of two kinds, **empirical** and **theoretical**. If only such parts are indicated as are present in the specimen under

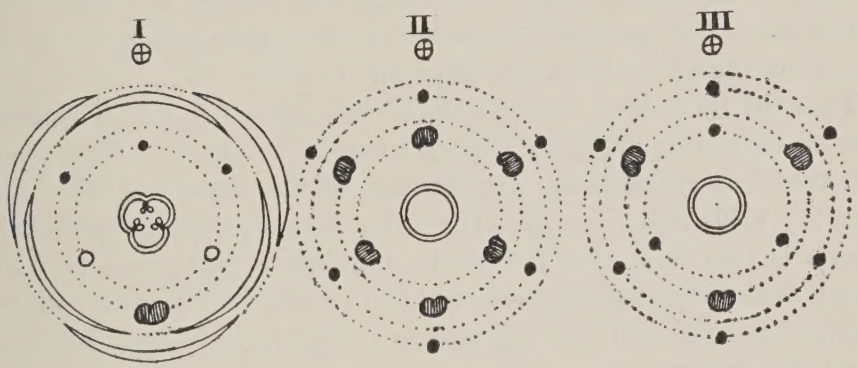


FIG. 159. Floral diagrams of some monocotyledons. I. *Orchis*. Only the anterior stamen of the outer whorl is functional, but two others belonging to the inner whorl are represented by staminodia in the flower and as circles in the diagram. The suppressed stamens are represented by dots. Placentation parietal. II. Bamboo. Six stamens, but no perianth. III. Most grasses. Inner whorl of stamens absent. No perianth.

observation, the diagram is described as an empirical one; but if an attempt is made by comparison with other plants and by the study of development to discover the general plan on which the flowers are constructed, and if the deviation of the special plant under consideration from the general plan is indicated in the diagram, a theoretical diagram is produced. Thus the floral diagram of the lily (Fig. 158, III) indicates the general plan on which a large number of monocotyledonous flowers are constructed; but various degrees of suppression have taken place, and the missing members may be indicated in the theoretical diagram by dots; in *Iris* (and other *Iridaceæ*) the inner whorl of stamens is suppressed (Fig. 158, I); in most orchids only the anterior stamen of the outer whorl is functional, but two others belonging to the inner whorl are represented by **staminodia** (Fig. 159, I);

in the bamboo all the stamens are present, but there is no perianth (Fig. 159, II), while in most grasses the inner whorl of stamens is entirely absent (Fig. 159, III). In an acyclic flower the floral leaves are represented on a spiral line.

Floral formulæ are used for much the same purpose as floral diagrams. The letters K, C, A, and G are used for the calyx, corolla, androœcium, and gynæcium respectively; each letter is followed by a figure showing the number of members in the series, or if the number is great by the symbol ∞. Cohesion is expressed by enclosing the corresponding figure in a bracket; adhesion by enclosing the adherent whorls in a common square bracket. If the number of members in a whorl is variable, this is indicated by the symbol *n*. Superior or inferior ovaries may be represented by drawing a line beneath or above the figure expressing the number of carpels in the gynæcium. If a perianth is present it is represented by the letter P, instead of the symbols for the calyx and corolla.

Thus the formula of most *Umbelliferæ* is K5, C5, A5, $G\overline{(2)}$, the last symbol indicating that the inferior ovary is composed of two carpels and that it is syncarpous; the formula of the *Cruciferæ*, K2+2, C4, $A2+2^2$, $G\underline{(2)}$, indicates that the calyx is polysepalous and in two whorls of two each, that the corolla consists of four petals in a single whorl, that the androœcium consists of two whorls, the inner one being duplicated, and that the gynæcium is bicarpellary and has a syncarpous superior ovary; the formula of the primrose, K(5), [C(5), A5], $G\underline{(5)}$, indicates the cohesion of the sepals and petals and the adhesion of the stamens to the corolla; K5, C5, A5+5, $G\underline{5}$ is the formula of the stonecrop (*Sedum*), in which the ovary is apocarpous; P3+3, A3+0, $G\overline{(3)}$, the formula of the *Iridaceæ*, indicates a two-whorled perianth, an androœcium in which the inner whorl is suppressed, and a tricarpellary inferior syncarpous ovary.

The Symmetry of the Flower.

If a flower can be divided into similar halves by section in one or more planes it is said to be **symmetrical**; if there is no plane of symmetry it is **asymmetrical**. The following degrees of symmetry are recognized:—

(*a*) **Radial** or **Actinomorphic.** In this case the flower is symmetrically divisible in two or more planes, the halves produced by section in one plane being similar to those produced along the

others. All the whorls of which the flower consists must contain the same number of members, and all the members of a whorl must be alike in size, form, &c., i.e. the flower must be **regular.** The tetramerous flowers of *Epilobium*, *Fuchsia*, &c. are divisible only in the medial and lateral planes into exactly similar halves, though they are also divisible symmetrically along the diagonal planes (Fig. 157, I); the flower of the lily has three planes of symmetry (Fig. 158, III); the geranium and many *Caryophyllaceæ* have five (Fig. 157, II, III); the hexamerous flowers of some *Sedums* are divisible symmetrically along twelve planes, but the halves produced by section along six of the planes are unlike those produced by section in the other six

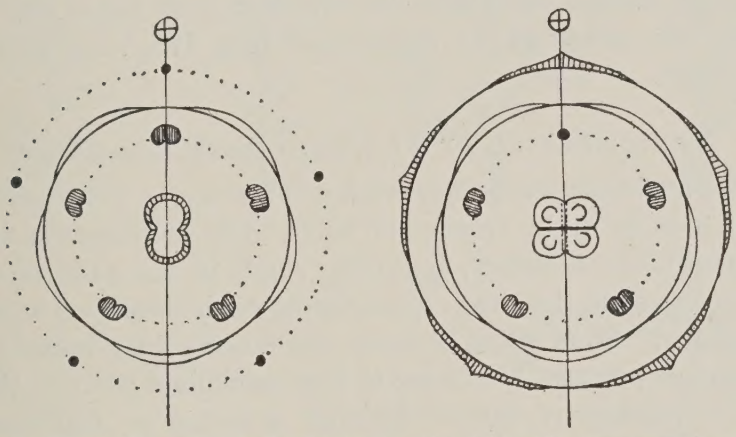


FIG. 160. Floral diagram of *Compositæ* on the left. The two carpels are median. Reduced calyx represented by dots. There is only one plane of symmetry—the median plane of the flower. Symmetry medianly zygomorphic. Floral diagram of most *Labiatæ* on the right. The posterior stamen is suppressed and represented by a dot. The two carpels are median, and are separated by a true septum, represented by the continuous line. The spurious dissepiment is indicated by a dotted double line. Symmetry medianly zygomorphic owing to reduction in andrœcium and gynæcium.

planes. All these flowers are described as possessing radial or actinomorphic symmetry.

(*b*) **Isobilateral.** In this case there are two planes of symmetry, but the halves produced by section along one plane are unlike those produced in the other. The flowers of the *Oleaceæ*, owing to reduction in the andrœcium and gynæcium, are diversely symmetrical in two planes (Fig. 158, IV), as are also the flowers of the *Cruciferæ*, &c. (Fig. 157, IV).

(*c*) **Monosymmetrical** or **Zygomorphic.** The flowers have but a single plane of symmetry. This is a very common condition, and may be produced in various ways; in many cases it is due to reduction in the number of members in one or more whorls, as in the *Solanaceæ*, *Boraginaceæ*, *Compositæ*, &c., in which the gynæcium is reduced to

two carpels. In the *Compositæ* (Fig. 160) the plane of symmetry is the median plane of the flower, and the flower is described as **medianly zygomorphic**; the plane of symmetry may also be lateral or oblique. Zygomorphism is also very commonly the result of **irregularity**, i. e. of the unequal development of the members of the same whorl, which is very commonly accompanied by reduction in the gynæcium or androecium, e. g. the *Labiatæ* (Fig. 160) and *Scrophulariaceæ*, in which the corolla is irregular (zygomorphic), the stamens reduced to four (generally), and the carpels to two. Such flowers may also be described as **dorsiventral**, the anterior part of the flower being different from the posterior, as is well shown in the *Orchidaceæ*, *Labiatæ* (in which the corolla has an upper and a lower lip), &c. The flower of the monkshood (Fig. 178, VI, p. 357) is also zygomorphic.

The Grouping of Flowers; Inflorescences.

In some angiosperms the flowers are borne singly, either terminating the main axis as in the crocus and tulip, when the flower is described as **terminal** and **solitary**, or arising singly in the axils of ordinary foliage leaves as in the violet, when the flower is described as **solitary** and **axillary**. More often, however, the flowers are grouped together (for attractive purposes) on more or less specialized parts of the plant, forming a number of definite **branch systems** or **inflorescences**. The inflorescence itself may be **terminal**, as in the foxglove (*Digitalis*), where the main vegetative axis is continued into the axis of the inflorescence; or **lateral**, as in the gooseberry and currant. The main axis of the inflorescence may or may not bear leaves (**bracts**) in the axils of which flowers, or other axes—secondary axes—arise; in the latter case the secondary axes may be merely the pedicels of the flowers, as in the currant and foxglove, or they may again branch, giving rise to complex branch systems, as in the oat (Fig. 162, I). Inflorescences are usually divided into two classes, **racemose** or **indefinite**, and **cymose** or **definite** inflorescences.

A **racemose** or **indefinite inflorescence** is one in which the main axis continues to grow until the development of the last flower; the flowers are developed in **acropetal succession** (i. e. from the base of the inflorescence upward; or where the axis is compressed and flattened, as in *Compositæ*, from without inward), and if a terminal flower is produced it is the last one to be formed and opened.

A **cymose** or **definite inflorescence** is one in which the growth of

the main axis is terminated by the formation of the first flower; a secondary axis (or axes) is produced below the apex of the main axis, and this also ends in a flower, and this process is repeated with the axes of successively higher orders.

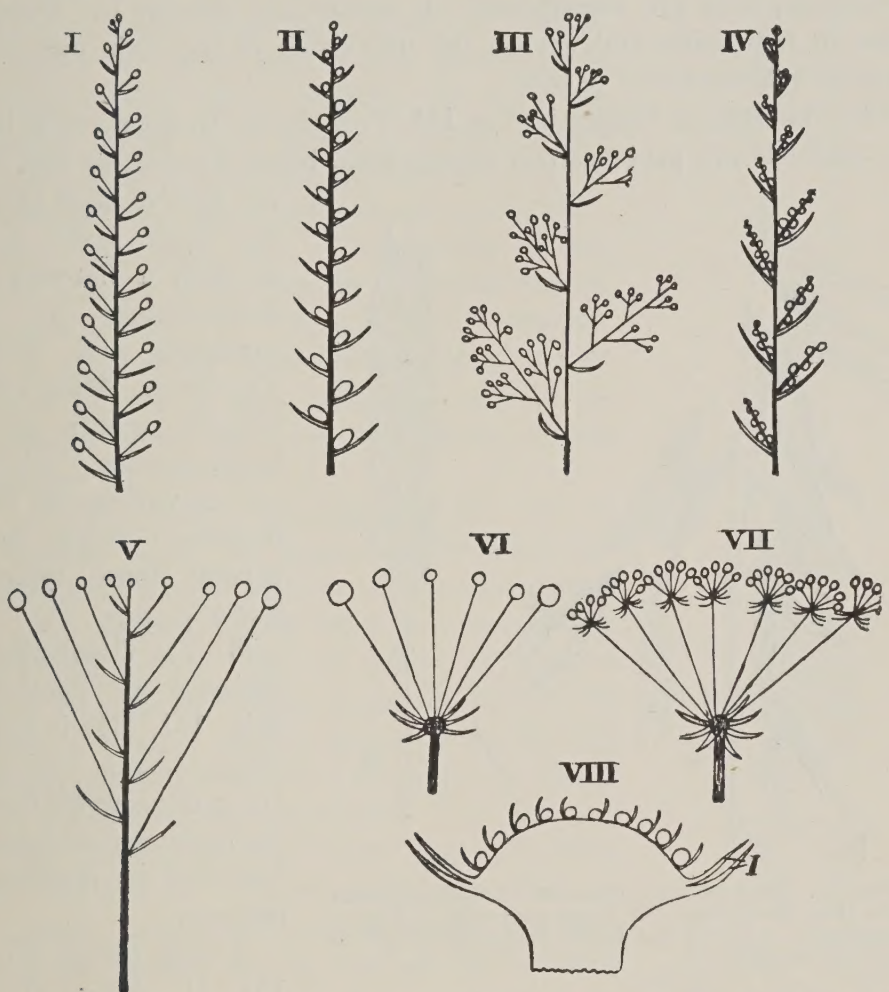


FIG. 161. Diagrams of racemose inflorescences. I. Simple raceme. II. Simple spike. III. Compound raceme. IV. Compound spike. V. Corymb. VI. Simple umbel. VII. Compound umbel. VIII. Capitulum or head. The bracts (involucre) I in VIII are always present. All the other bracts shown may be either present or absent.

(A.) RACEMOSE INFLORESCENCES.

The following varieties are usually recognized:—

(1) The **Simple Raceme** (Fig. 161, I), as in the foxglove, currant, barberry, &c. The main axis of the inflorescence, known as the **peduncle** below the lowest flower, and as the **rhachis** between the

flowers, is elongated and bears stalked (**pedicellate**) flowers developed in acropetal order. The pedicels attain approximately the same length. Bracts may or may not be developed; in the former case, as in the foxglove, the flowers are **bracteate**; in the latter, as in *Cruciferæ*, they are **ebracteate**. If bracts are present the flowers arise in their axils, and not on the other side of the main axis (cp. cymose inflorescences, p. 302).

(2) The **Simple Corymb** (Fig. **161**, V) is similar to the raceme, but the pedicels are progressively shorter from below upward, so that all the flowers lie at about the same level, and so form a flat-topped inflorescence, as in candytuft and other *Cruciferæ*. Many cruciferous plants have inflorescences which are corymbose in the flowering stage, but become more typical racemes later.

FIG. 162. Inflorescences of grasses. I. Spicate panicle of the Oat. A=spikelet. II. Compound spike of Wheat. A=spikelet. A few of the lowest spikelets (or spikes) have been removed.

(3) The **Compound Raceme** or **Panicle** (Fig. **161**, III) is produced when the secondary axes given off from the main axis are again branched in a racemose manner.

(4) The **Spike** (Fig. **161**, II) differs from the raceme in that the flowers are sessile or nearly so, and may be bracteate or ebracteate, e.g. agrimony, plantain, &c. The small dry spikes of grasses are known as spikelets.

(5) The **Compound Spike** is formed when the main axis of the inflorescence bears lateral spikes instead of single flowers. This is the case in some grasses, such as wheat (Fig. **162**, II).

(6) The **Catkin** or **Amentum** is a spike of inconspicuous unisexual flowers; the spike as a whole falls off after flowering, e.g. alder, birch, hazel (Fig. **192**, p. 404), oak, willow, &c. The catkins are

described as either male or female according as they bear staminate or carpellary flowers.

(7) The **Spadix** also bears inconspicuous unisexual flowers, but the main axis is thick and fleshy. A good example is seen in the common *Arum maculatum* (lords and ladies), in which the lower part of the spadix bears female flowers each consisting of a single carpel; above these are the closely packed male flowers, and still higher some sterile male florets forming downwardly directed hairs (Fig. 163). The upper part of the spadix in this case (but not in all cases) is sterile and has an attractive function. The spadix is enveloped in a large leafy bract known as a spathe (Fig. 174, III, p. 345), which is green in the common arum, but white (**petaloid**) in the trumpet lily (*Richardia*).

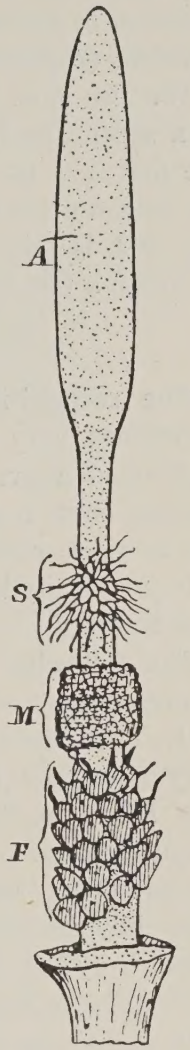


FIG. 163. Spadix of the wild Arum. The spathe has been removed in order to show the flowers. A = the upper sterile and attractive part of the spadix; F = female flowers, each consisting of a single carpel; M = male flowers; S = downwardly directed hairs representing partially aborted flowers.

(8) The **Simple Umbel** (Fig. 161, VI) is produced when the internodes between the pedicellate flowers are not elongated, so that all the flowers spring from the end of the peduncle at one level. If bracts are present they form an **involucre** round the base of the umbel. Simple umbels are seen in the ivy, cherry, some *Umbelliferæ*, &c. In the cherry the peduncle is also suppressed.

(9) The **Compound Umbel** (Fig. 161, VII). In this case we have an *umbel of umbels*, as in most *Umbelliferæ*. An involucre of bracts may be present at the base of the primary umbel (**general involucre**), or below each secondary umbel (**involucels** or **partial involucres**).

(10) The **Capitulum** or **Head** (Fig. 161, VIII) is produced when the main axis remains short (as in the umbel) and the flowers are also sessile. The bracts of the individual flowers (the flowers are also known as *florets*) may be present as leaves or scales on the receptacle, and are known as **paleæ**, but

commonly they are absent; in all cases the whole inflorescence is surrounded by an **involucre**. The capitulum is characteristic of the *Compositæ* (daisy, dandelion, sunflower, &c.), but is also found in the scabious (*Dipsaceæ*), clover, &c.

We also have **racemose mixed inflorescences** when the branches of a second (or higher) order do not develop in the same manner as the first, e. g. the **spicate panicle**, in which a number of short spikes are borne on a branched raceme, as in many grasses (e. g. the oat, Fig. 162, I); the **capitulate raceme**, as in the butterbur (*Petasites*), in which a number of capitula are arranged in a raceme, &c.

(B.) Cymose Inflorescences.

The recognition of the cymose character of an inflorescence is sometimes very easy but is often difficult; nearly all the forms mentioned above as racemose inflorescences may be simulated by cymose ones, e. g. we have cymose racemes, cymose umbels, &c., and in some cases, owing to the absence of bracts and other causes, it is practically impossible to determine whether the inflorescence is racemose or cymose.

The following are some of the varieties of cymose or definite inflorescences:—

(1) The **Dichasial Cyme**, which is typically developed in many *Caryophyllaceæ* (e. g. stitchwort, chickweed, *Gypsophila*, ragged robin, Fig. 181, I, p. 365). Two equal branches are developed below the terminal flower; each of these ends in a flower, and lateral branches are produced repeating the arrangement on the main axis. It is commonly the case that the dichasium ultimately passes into a monochasium by the non-development of one out of the two branches in the higher orders of branching (Fig. 164, I). There is no distinct main axis to the whole inflorescence.

(2) The **Scorpioid Cyme**, which is characteristic of the *Boraginaceæ*, *Crassulaceæ*, &c. This is monochasial, as only one branch is developed on each relative main axis; these occur alternately on opposite sides (Fig. 164, II). Parts of the successive axes form a main axis (*pseud-axis*), which is therefore a **sympodium** (Fig. 164, III). An inflorescence of this kind may look very like a raceme, and if the bracts are absent cannot be distinguished from such; if however bracts are present, they will be found on the opposite side of the stem to the corresponding flowers, because the various segments of the main axis and not the flowers are in the axils of the leaves.

In many *Boraginaceæ* the two rows of flowers (each a branch of a *dichasium*) occur on the upper side, and the two rows of bracts on the lower side, of the rolled-in sympodium. In the comfrey (Fig. 188, I, IV, p. 391), forget-me-not, and some other *Boraginaceæ*, the bracts are absent and the inflorescences may be racemose.

(3) The **Helicoid Cyme** (Fig. 164, IV, V) is also monochasial, but

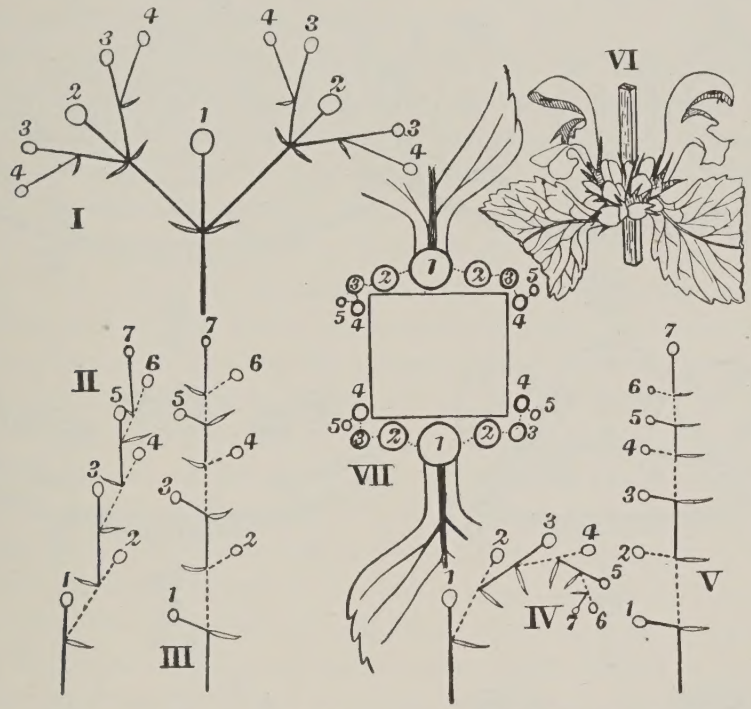


FIG. 164. Diagrams of cymose inflorescences. I. Dichasial cyme passing into a monochasial one, as is commonly the case. Typically shown in many *Caryophyllaceæ*. The figures indicate the order of development of the flowers. II. Scorpioid cyme. A monochasium in which the branches arise alternately on opposite sides. III. The same straightened out, showing the origin of the pseud-axis or sympodium, which is formed of portions of successive axes. Note the position of the leaves on the opposite side of the main axis to the flowers. IV. Helicoid cyme. Also a monochasium, but the branches are all on the same side. V. The same straightened out and forming a sympodial axis. VI. Verticillaster of the Dead-nettle. VII. The same shown diagrammatically by a transverse section at a node. The inflorescence is a dichasium with sessile (or nearly sessile) flowers. After the first branching it becomes monochasial. The figures indicate the order of opening of the flowers.

the lateral branches always occur on the same side. A *pseud-axis* is formed as in the scorpioid cyme, so that the inflorescence looks like a one-sided raceme.

(4) The **Verticillaster** is the name given to the peculiar inflorescence found in many *Labiatæ* (e. g. the dead-nettle, Fig. 164, VI). The leaves are opposite and the flowers appear to form a whorl; it will be found, however, that they are really in two groups, one belong-

ing to each leaf. The central flower of each group opens first; this is followed by two others, one on either side of the central one, and these by others as represented in Fig. 164, VII. The inflorescence is really a dichasium in which the flowers are sessile or nearly so, and which,

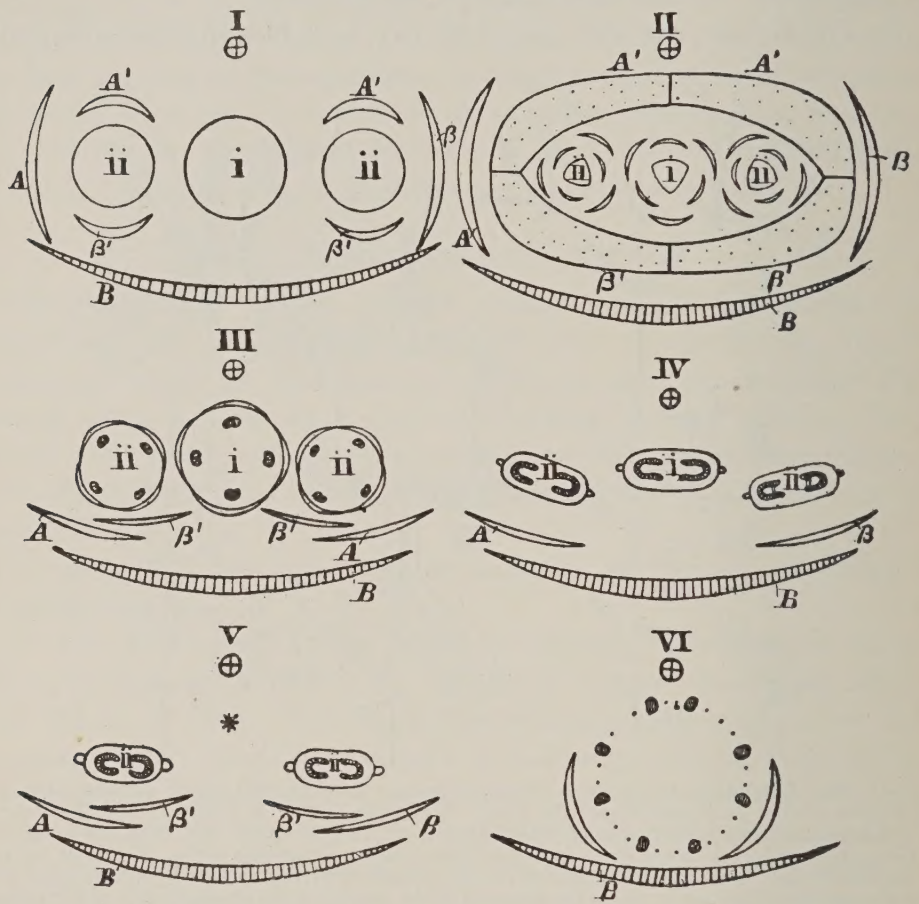


FIG. 165. Diagrams showing the arrangement of the flowers in various *Cupuliferæ* (see text). I. Typical arrangement. II. One of the scales with included flowers from a female catkin of the edible Chestnut (*Castanea*). Each flower has a perianth of six leaves. III. Ditto from the male catkin of the Alder (*Alnus*). IV. Ditto from the female catkin of the Birch (*Betula*). V. Ditto from the female catkin of the Alder (*Alnus*). VI. Ditto from the male catkin of the Hazel (*Corylus*). B=scale or bract in the axil of which the flower i arises with its bracteoles A and β. In the axils of A and β the flowers ii, ii arise with the bracteoles A′ β′, A′ β′. * indicates a missing flower.

as is usually the case, soon becomes monochasial. The Glomerule of the box (*Buxus*) is essentially similar.

(5) The inflorescence of many of the *Cupuliferæ*, although commonly described as a simple catkin (see above), is really made up of a number of cymes, one in the axil of each scale of the catkin.

The typical arrangement is shown in Fig. 165, I, where B is one of

the scaly bracts of the catkin; in the axil of this leaf the sessile flower i arises with its lateral bracteoles A and β, in the axils of which the flowers ii, ii arise with two more bracteoles A′ and β'. This complete condition is realized in the female catkins of the Spanish or edible chestnut (*Castanea*, Fig. 165, II), where the bracteoles A′, β', A′, β' are thick and coherent, forming a prickly cupule which completely encloses the fruit until it is ripe.

Various degrees of reduction take place: in the male catkin of the alder (*Alnus*, Fig. 165, III) each scale encloses three flowers, but only four (not six) bracteoles, those indicated by the symbols A′, A′ in Fig. 165, I, being absent; in the female catkin of the birch (*Betula*, Fig. 165, IV) only the bracteoles A and β are present. The flowers may also be reduced in number; in the female catkin of the hazel (*Corylus*, Fig. 192, VIII, p. 404) the uppermost scales each enclose but two flowers, the middle one of the cyme being aborted, and six bracteoles, the three on either side forming the characteristic leafy cupule surrounding the corresponding fruit (nut); in the female catkin of the alder also two flowers are developed (Fig. 165, V), but only four bracteoles; in the male catkin of the hazel only the central flower is developed with two bracteoles (Fig. 165, VI); in the male catkin of the oak (*Quercus*) each bract bears only a single flower without bracteoles.

(6) The **Cymose Corymb.** This is seen in the hawthorn and guelder rose, the inflorescences of which are shown to be cymose by the fact that some of the *inner* flowers open first, instead of last.

(7) The **Cymose Umbel** is produced when a number of lateral axes are developed in a whorl on a main axis which first ends in a flower. This is seen in the *Pelargonium*, and is distinguished from the simple racemose umbel by the order of opening of the flowers.

(C.) Mixed Inflorescences.

Mixed inflorescences are those in which one order of branching is racemose and the other cymose. Of these there are many kinds, and they are often difficult to understand. Thus in the horse-chestnut (*Æsculus*) we have a raceme made up of scorpioid cymes; in chicory (*Cichorium*) the capitula are arranged in a cymose manner; in *Cineraria* the capitula form a corymbose cyme, &c.

CHAPTER XVIII

THE POLLINATION OF FLOWERS

A SHORT account of pollination has already been given (supra, p. 134); in this chapter some further details will be given of some special arrangements for ensuring either self- or cross-pollination as the case may be.

The advantage of **cross-pollination** (and subsequent **cross-fertilization**) over **self-pollination** has been abundantly proved in many cases by the better seed, and consequently more vigorous and fertile offspring produced. So far, indeed, has Nature gone in this direction, that in some instances we have the remarkable case of plants which are absolutely sterile to their own pollen, i.e. the pollen of the plant is incapable of fertilizing the oospheres of its own ovules. On the other hand, a great many plants are habitually self-pollinated and fertilized, and special modifications may be present to ensure this.

It is clear that all **unisexual flowers** (e.g. many forest trees, species of campion (*Lychnis*), sedge (*Carex*), *Mercurialis*, &c.) must be cross-pollinated, because the stamens and carpels are in separate flowers, or even (when the plant is dicœcious) in separate individuals. In a large number of trees (oak, birch, pine, hazel, alder, &c.), as well as in grasses and sedges, a very large quantity of light dry pollen is produced, which is wafted about in the air by the wind, some of it finally reaching the branched hairy stigmas of the female flowers (see *Cyperaceæ*, Fig. 175, II, IV, p. 347). Such **wind-pollinated** (**anemophilous**) flowers are commonly small and inconspicuous, destitute of a perianth, or at least without a brightly coloured one, and they often open in early spring before the unfolding of the leaves, which would otherwise interfere with the dispersal of the spores, or pollen grains. In most plants in which the flowers are brightly coloured and conspicuous either by their colour or size, or by the production of sweet nectar or perfume, cross-pollination is brought about by animals (generally insects, hence **entomophilous**), which visit the flowers in search of honey or pollen and carry some of the latter away with them. The honey is produced in glandular organs known as **nectaries**, which are very variously placed on or in different parts of the flower. Some-

times the nectar is contained in long hollowed structures known as **spurs**, which may belong to the calyx (e.g. *Tropæolum*) or to the corolla (e.g. larkspur, *Orchis*, monkshood, columbine, &c.). In the wallflower and other *Cruciferæ* the nectaries lie around the bases of the two outer shorter stamens and are therefore staminal, but the honey collects in the somewhat pouched bases of the inner sepals which lie opposite to them. Another good example of a staminal nectary is seen in the violet, in which outgrowths of the two anterior stamens secrete honey which collects in the spur of the anterior petal (Fig. 166, p. 313). In *Ranunculus* a nectary is borne at the base of each petal (Fig. 178, II, p. 357); in the grass of Parnassus (*Parnassia*), a bog plant belonging to the *Saxifragaceæ*, the five inner stamens are represented by nectar-secreting branched staminodes; in the garden lily the honey is secreted in a groove running down each perianth leaf. In many monocotyledons the nectaries lie in the septa of the multilocular ovary (**septal glands**), while in yet other cases the nectary forms a **disc**; this may be developed over an inferior ovary (e.g. *Umbelliferæ*), or as a ring of tissue surrounding the base of a superior ovary (e.g. *Euonymus*, *Erica*, *Labiatæ*, &c.), or a lateral scale (e.g. mignonette), or as a whorl of rounded prominences around the flower (e.g. *Nerium Oleander*, &c.).

In most cases the nectaries and stamens are so placed that the dehiscence of the anthers takes place *towards* the nectaries, i.e. when the nectaries are towards the centre of the flower the anthers are introrse, but when, as in the buttercup, the nectaries are towards the outside of the flower the dehiscence of the anthers is extrorse, or at least lateral. It should be remembered, however, that insects (e.g. bees) may visit flowers not only to collect the sweet nectar, if present, but also for the sake of the pollen itself, which is used as food; when flowers such as the poppy and buttercup are visited for this purpose a large amount of pollen must be produced in order to make up for the large quantity which is lost so far as the plant is concerned. It is obvious, however, that some of the pollen which is being collected by insects is likely to be left on the stigmas of other subsequently visited flowers and so bring about cross-pollination.

Flowers such as the orchids, which are visited by insects (and which are indeed often absolutely dependent on such visits for their pollination), but in which the insects do not seek the pollen itself, produce pollen in relatively small amount, as only a small quantity is likely to be lost compared with the large amount wasted in anemo-

philous plants and in flowers which are visited for the sake of their pollen.

The methods adopted by plants to ensure insect visitation and cross-pollination are many and various: e.g. bright and therefore conspicuous colours either in flowers of great size or by the massing together of smaller flowers; variegation of flowers; sweet juice which may or may not be scented, &c. Some insects appear to have a distinct partiality for flowers of particular kinds and even for particular colours, e.g. flies prefer pale, dull, spotted flowers with (to us) unpleasant odours, while bees like bright-coloured flowers with pleasant odours. It is interesting to note that a number of the largest, most brightly coloured and variegated flowers are quite or nearly scentless, while many with highly perfumed nectar have comparatively inconspicuous flowers, which, even if coloured, are not variegated. Compare, for example, the scentless pansy with the sweet violet, two closely related plants; the sweet-scented mignonette and *Daphne* with the showy *Tropæolum* and poppy, &c. It would seem that in such cases the one form of attraction renders the other less important, and the energy of the plant is therefore not wasted in its production.

The form of an insect-pollinated flower often shows very clear adaptation to that of the particular insects or other animals by which it is habitually pollinated; it is often such as to compel the insect to alight on the flower at a particular spot and to take up such a position and make such movements as will almost certainly result in the deposition of pollen on a definite portion of the insect's body, and this the part which will also come into contact with the stigma of the next flower of the same kind visited. In this way insect structure has been gradually modified through the influence of flowers, and flower-structure, colour, &c., has been modified by insects. By the agency of natural selection, brightly coloured or sweetly scented flowers by being attractive to insects have been more certainly pollinated and their offspring maintained than those which have not so varied. As a result of this such plants have become more numerous, and every variation in structure favourable to insect visitation has been perfected and perpetuated. Conversely, only insects adapted by their structure to reach the nectary of the flower could obtain their food and live to procreate their progeny; the others have disappeared in the struggle for existence. Indeed it is probably not too much to say that insects have selected and preserved, in a sense, our showy blossoms and that

without their agency all our flowers would have remained as inconspicuous as our wind-pollinated ones are.

The variegation of flowers by dots, lines, and streaks is another contrivance to facilitate insect visitation; examination of a number of such flowers (e. g. the pansy, *Tropæolum*, &c.) will show that the dots, lines, &c., are so arranged as to point the way to the nectary or nectaries, and they are probably of use to insects in this way. Such flowers are frequently visited by quite small insects to which **directing lines** are especially useful, particularly so as such flowers are commonly nearly or quite scentless. The insects are thus led to follow a definite track in the flower during which they come into contact with the anthers and pollen.

Many different kinds of insects are brought into use in this way; when a flower has a long tubular corolla and the honey is contained at the base of it (e.g. the pinks), or where the nectar is contained in a long spur (e. g. honeysuckle), only insects which have a long proboscis, such as butterflies, bees, wasps, &c., are capable of reaching the honey, and in such cases there can be little doubt that the insects are as much modified and adapted to the form, &c., of the flowers from which they obtain their honey, as the flowers are to the insects by which they are pollinated. Flies and beetles have but a short proboscis, and are therefore most useful to flowers in which, as in the buttercup, the nectar is superficial. Many flowers are pollinated at night by moths and large beetles, and such flowers are commonly white in colour and so are easily seen in a weak light (e.g. the great convolvulus of the hedges), or they open only at night as in the evening primrose and Nottingham catchfly (*Silene nutans*). All insects are not equally useful in the work of pollination; small crawling insects often do more harm than good, as any pollen which they may carry will be likely to be rubbed off and so wasted before the insect reaches another flower of the same species.

In some cases animals other than insects are employed: spiders, snails, and even birds (**ornithophilous pollination**). Hummingbirds are of some considerable importance in connexion with the pollination of the gaudy trumpet-flowers (*Bignonia*, &c.) of tropical America.

The flowers of some aquatic plants are pollinated in the water, and are therefore described as **hydrophilous.** The pollen (or in some cases the male flowers) of such plants is liberated and floats on the surface of the water where pollination takes place. A good example

of a hydrophilous plant is found in *Vallisneria*, which is described on p. 316.

Dichogamy. In many hermaphrodite flowers the stamens and carpels do not come to maturity at the same time, so that when the anthers are ripe and the pollen is being shed the stigmas are not in a receptive condition, either because they are immature, or because they have passed maturity and are no longer susceptible to pollination. This condition is described as **dichogamy**, and is obviously of great importance in securing cross-pollination, inasmuch as a flower must necessarily be pollinated, if it is pollinated at all, by pollen brought from another flower in a slightly older or younger condition as the case may be. In most dichogamous flowers the anthers come to maturity before the stigmas, in accordance with the normal acropetal order of succession of the floral whorls; this condition is described as **protandry**, and is found in the flowers of *Campanula* (the bell-flowers), stitchwort (and most *Caryophyllaceæ*), *Labiatæ*, *Compositæ*, *Umbelliferæ*, &c. In some flowers, however, the acropetal order of development is reversed, and the stigmas become mature and receptive before the anthers of the same flower are ripe; this is described as **protogyny**, and is comparatively rare, but is found in the plantain, *Arum*, *Parietaria*, the forget-me-not, &c. It is clear that in protogynous flowers the chance of self-pollination depends on the length of time during which the stigmas remain fresh and receptive: self-pollination is only absolutely excluded if the stigmas come to maturity and wither before the pollen is shed; in those cases in which the stigmas remain receptive for a long time pollen from the same flower may of course fall upon them.

Heteromorphism. Another interesting contrivance is seen in those plants which have flowers of two or three different kinds, with structural differences in the length of the styles and position of the stamens of such a nature as to facilitate cross-pollination. The best known example of this is the primrose, which is **dimorphic**, i.e. has flowers of two kinds, some with the stamens inserted low down in the tube of the corolla and the knob-like stigma at its mouth, and the others with the parts exactly reversed, i.e. the stigma about halfway down the tube and the anthers at its mouth. There are therefore **long-styled** and **short-styled** primrose flowers, and the same heteromorphism occurs in the cowslip, oxlip, flax, lungwort, &c. The observations and experiments of Darwin and others have shown that if primroses are carefully protected from insect visitation little or no

seed is produced; also that better seed is set when a short-styled flower is pollinated from a long-styled one, and vice versa, than is the case when the pollen comes from a flower of the same form, whether it be on the same plant or on another one. It is easy to realize the action of insects in the transference of pollen from one form to another: suppose that an insect (such as a moth or other insect with a long proboscis) first visits a flower in which the stigma is low down in the tube and the anthers high—it will send its proboscis down to the bottom of the tube after the honey, the pollen of the anthers will adhere round the base of the proboscis, and occupy precisely the position that will come into contact with the stigma of the next flower visited, should that chance to be a long-styled one. Should the flower first visited be a long-styled one, the pollen will adhere at a level closer to the end of the proboscis, and will come into contact with the stigma of the next short-styled flower visited. But there can be little doubt that the visits of insects to flowers of this kind must, in a great many cases, result in self-pollination by the shaking, &c., which takes place during the search for the nectar, and of course self-pollination is far better than no pollination at all, which is the result of insect exclusion. The chances of self-fertilization are, however, much reduced, when we remember that the pollen from a flower of a different form is prepotent over that from the same flower, i.e. it has more power to effect fertilization. It is therefore probable that cross-fertilization occurs whenever it is possible, i.e. when the appropriate pollen grains have been deposited on the stigma, and that if such grains are not present the flower is likely to be self-fertilized. It is interesting to note that larger pollen grains are produced in the short-styled forms than in those with long styles, apparently because longer pollen-tubes are needed to penetrate the styles of the form (the long-styled one) on which the grains will germinate.

Some few plants are **trimorphic**, i. e. have three forms of flowers with three different lengths of styles and filaments of stamens. Examples are found in the purple loosestrife and in some species of *Oxalis*. The purple loosestrife (*Lythrum Salicaria*) has handsome terminal spikes of hexamerous flowers exhibiting trimorphism of the styles and stamens. The latter are in two whorls, and different plants may have: (1) flowers with a long style and medium and short stamens; (2) flowers with a style of medium length associated with long and short stamens; or (3) flowers with a short style and medium and long stamens. Insects visiting the flowers naturally touch the stigmas

with the same parts of their bodies which have been previously dusted with pollen from one of the other forms, and Darwin has shown that the pollen from a stamen is prepotent on the stigma of a flower with a style of the same length as the stamen.

Cleistogamous Flowers. A remarkable adaptation having self-pollination and fertilization for its object is found in those plants which produce two entirely different kinds of flowers: some large, conspicuous ones adapted to cross-pollination by insects; and others which are small, inconspicuous, green, and bud-like, and which, although self-pollinated, produce abundance of seed. Such closed (**cleistogamous**) flowers are found in the violet (*Viola*), wood-sorrel (*Oxalis Acetosella*), &c., and as would be expected their petals are either very small or absent altogether. The anthers of such flowers are small, as no pollen is wasted, and the pollen grains germinate while within the anther; and there is no honey or scent as no insects are to be attracted. Cleistogamous flowers appear late in the season, generally after the conspicuous flowers have disappeared. The advantage to the plant of the possession of such flowers appears to lie in the certainty with which abundance of seed is produced with the least possible expenditure of material, and the safeguard which the plant thus has in case of the sterility of the more conspicuous flowers, which run considerable risk of non-pollination at the early period of the year at which they are produced. Of all the British species belonging to the genus *Viola*, the sweet violet (*V. odorata*), dog violet (*V. canina*), hairy violet (*V. hirta*), marsh violet (*V. palustris*), and heartsease or pansy (*V. tricolor*), the last is the only one in which the showy flowers commonly produce seed.

THE FOLLOWING ARE SOME SPECIAL POINTS IN CONNEXION WITH THE POLLINATION OF THE PLANTS NAMED:—

Barberry. In this plant the bases of the stamens are irritable, so that when an insect alights on the flower and touches the stamens, they spring forward and project the pollen on to its back, at the same time commonly startling the insect, so that it flies away to another flower without waste of time.

Violaceæ (see p. 363). The honey is secreted by two outgrowths of the anterior stamens which project into the spur of the anterior petal, the entrance to which is partly blocked by the upper expanded or hooked end of the style. The flowers hang downward, and the

prolongations of the connectives of the anthers enclose a space within which the pollen collects as it escapes from the introrse anthers. In the heartsease (*Viola tricolor*) the stigma is situated in a pit beneath which is a hinged lid. When an insect visits the flower and seeks for the honey in the spur it is likely to leave some pollen from a previously visited flower on the freely exposed stigmatic surface or pit, while its movements lead to some of the pollen being shaken out of the space between the connectives on to the insect's head or proboscis. On withdrawing from the flower the hinged lid closes over the stigmatic surface, and so shields the latter from pollen produced in the same flower, i. e. from self-pollination.

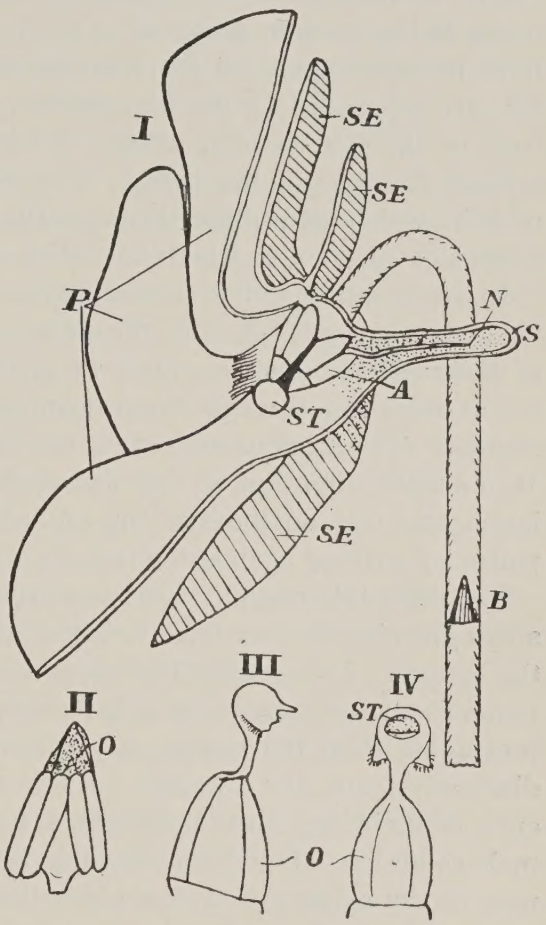


FIG. 166. The Pansy or Heartsease (*Viola tricolor*). I. Flower in natural position for pollination. The sepals and petals of one side have been removed, and the spur is shown in median section. A=anthers; B=one of the two lateral bracteoles or prophylla; N=nectary; P=petals; S=spur; SE=sepals; ST=stigma. II. Two of the slightly syngenesious stamens with their outgrowths (O) above the anthers. III, IV. Side and front views of the pistil. O=ovary; ST=stigmatic surface.

Leguminosæ (see pp. 23, 376, for an account of the structure of the flowers in this order). In the scarlet runner (*Phaseolus*), pollination is effected by insects with long probosces (such as bees), as the honey is contained at the bottom of the long tube formed by the diadelphous stamens, and these surround the pistil and style. The stamens and pistil are contained in the keel of the corolla, and when the anthers ripen some of the pollen is shed into the end of the staminal tube. An insect visiting such a flower alights on the wings and depresses them as well as the keel to which the wings are locked.

The effect of this movement is to cause the protrusion of the style and some of the pollen through a small aperture at the end of the carina on to the insect's breast. The pollen is thus deposited on the insect's body in such a position that it will be likely to pollinate the stigma of the next flower visited. The insect gets to the honey by partly lifting the free posterior stamen. Forms of *Leguminosæ* which have no honey have all the stamens united. The red clover, vetch, &c., are pollinated by the humble-bee. Two small apertures at the base of the free stamen afford entrance to the nectary which lies around the base of the ovary. The style is provided with a brush of hairs which, as it glides through the canal at the end of the keel, sweeps out the pollen which has fallen there on to the insect's body.

In some forms with a monadelphous androecium (e. g. the furze) no honey is produced, and the flowers are only visited for the sake of their pollen; but in others (e. g. the broom) honey is produced and is accessible through small openings at the base of the posterior stamen. The stamens are not all of the same length, and the flower is in a state of tension, so that during the movements produced by an insect alighting on the alæ the anthers are caused to liberate their pollen by striking against the insect's body.

Plantain (*Plantago*). This is a typical anemophilous plant. The small greenish flowers form a dense spike with the oldest flowers at the bottom. It is markedly protogynous so that each hermaphrodite flower is at first physiologically female, and only the stigma is seen protruding from the almost closed flower, while later on the stigma disappears, and the versatile anthers are observed swinging at the ends of their long slender filaments, so that the flower is now in its male condition. It follows from this that as the flowers on the lower part of the spike are always older than those above, the lower part will usually be found in the male, and the upper in the female condition, so reducing the tendency of the latter to be pollinated from another flower of the same spike, while the wind can readily carry the light dry pollen to the flowers of other inflorescences. Owing to the marked protogyny self-pollination is practically impossible.

Hazel (*Corylus*). This plant also is typically anemophilous. The male catkins (see Fig. 193, I, p. 404) readily swing in the least breeze, and as they are formed before the foliage leaves there is nothing to prevent the very light dry pollen grains from being wafted on to the red stigmas of the female flowers.

Sage (*Salvia*). Fig. 189, III, p. 395. This genus belongs to the

Labiatæ, and several exotic forms are cultivated for the sake of their flowers. Two stamens only are present, and these are modified in order to assist cross-pollination by insects: each stamen has a short filament which is attached to a much elongated connective. The connective is broadened in most *Labiatæ*, but in the sage this is carried to an extreme degree with the result that the two anther-lobes are widely separated, so that when the stamen is in the natural position one lobe is in the upper lip of the corolla, while the other (which contains no pollen) comes to lie in the neck of the corolla tube. When an insect alights on the flower with the object of obtaining honey from the base of the corolla tube, it pushes against the sterile anther-lobes of the two stamens, and causes the connectives to swing round on the filaments with the result that the fertile lobes come down on the insect's back and deposit pollen there. The flowers are markedly protandrous. In the young condition the stigmas lie high up and are covered by the upper lip of the corolla; in the older condition, owing to elongation of the style, the stigmas take up the position occupied by the depressed fertile anther-lobes of the younger flower. When therefore an insect visits such a flower in the older condition, the stigmatic lobes sweep off the pollen and are pollinated.

Scarlet Pimpernel (*Anagallis arvensis*). This pretty little plant belongs to the *Primulaceæ*, and is generally seen widely open during fine weather only. Cross-pollination may take place during the first few days after its opening; if not the flowers close up permanently, the anthers come in contact with the stigma and self-pollination is effected.

Lords and Ladies (*Arum*), (see Figs. 163, 174, 111, pp. 301, 345). This plant is fertilized by small crawling insects which pass in at the open end of the spathe, and become prisoners owing to the presence of a number of short, downwardly directed hairs (barren flowers), which project into the narrow part of the tube. In wandering about among the unisexual (female) flowers at the bottom of the spathe they will, if they have brought some pollen from a previously visited flower, deposit some of it on the sticky stigmas. The plant is protogynous, and not until the anthers are ripe and the insects are dusted with pollen are they allowed to crawl out by the withering of the hairs; they may then visit another flower in the 'female condition' and so effect cross-pollination.

Orchid (*Orchis*). See p. 352 and Fig. 177 for a general description of the morphology of the flower in the *Orchidaceæ*. This family includes

the most perfectly adapted entomophilous plants known, and many of them are perfectly sterile to their own pollen. When an insect (e.g. a bee) visits a flower it alights on the platform or labellum, and proceeds to search for the honey contained in the spur. In passing its proboscis down the spur its head comes into contact with the rostellum and with the sticky bases of the caudicles of the pollinia. As the insect's head is kept in this position for some considerable time, the pollinia become firmly adherent to it, and, when the insect withdraws, the pollinia are removed from the anther-lobes, and the animal flies off with them to another flower. During the time required for the passage from one flower to another, the pollinia which are at first erect bend down forwards so that they strike the stigma of the next flower visited; a few of the sticky pollen-groups (massulæ) adhere to the stigma—the rest are carried away to other flowers so that there is but little waste of pollen. The removal of the pollinia by an insect can be imitated by taking a pointed pencil and pressing it against the rostellum; the pollinia will adhere to the top of the pencil and may be removed and the subsequent bending observed. Other orchidaceous plants show still more remarkable arrangements for ensuring cross-pollination; some, however, in spite of the extreme specialization of the flowers, are normally self-pollinated. The well-known bee orchis (*Ophrys apifera*) is one of the latter, as its weak caudicles sway forward so as to allow the pollen grains to adhere to the stigma of the same flower.

Vallisneria spiralis is also an interesting plant in this connexion. It is a common dicœcious weed in ponds and ditches of the warmer parts of Europe, and is sometimes seen growing in the sand at the bottom of an aquarium. The female flowers are borne on long slender stalks which raise the flowers to the surface of the water. The male flowers are borne on short stalks, and so are below the surface. When the female flowers are ready for pollination the male flowers break away from their stalks and float up to the surface of the water where pollination takes place. The long stalks of the female flowers then become spirally wound and thus draw the female flowers under water where ripening of the seeds takes place.

CHAPTER XIX

FRUITS AND SEEDS AND THEIR DISPERSAL

THE FRUIT.

THE subject of fertilization, and of the changes produced by the sexual act, whereby the ovule develops into a seed, and the ovary, with or without neighbouring structures, into a fruit, has been discussed in an earlier portion of this work in connexion with the types described (pp. 134, 140). The great diversity which exists, however, among fruits, renders a fuller treatment and a classification desirable.

A fruit, in the angiosperms, is defined as the product formed by the growth or persistence of any part of the flower, or of the neighbouring structures, as a result of the act of fertilization. Such a fruit encloses one or more partially developed embryos or seeds produced from the ovules (macrosporangia) as a result of the fertilization of the oospheres.

If the fruit is developed from the gynæcium alone it is described as a **true fruit**; if other organs of the flower (the calyx, receptacle, &c.), also take part in its formation, as in the apple, rose, &c., it is convenient to apply the term **false fruit** or **pseudocarp.**

When a fruit represents the growth of a single ovary, whether the latter represents a single carpel as in the cherry, pea, and barberry, or a number of coherent (syncarpous) carpels, as in the lily, primrose, &c., it is described as **simple**; when, as in most *Ranunculaceæ* and *Rosaceæ*, the gynæcium is apocarpous, the fruit is apocarpous also, each fruitlet representing a carpel. Such an apocarpous aggregation, which is the product of a single flower, is called an **aggregate fruit or etærio**; in other cases (e. g. the pineapple, fig, mulberry, sunflower, &c.), the apparent fruit represents not a single flower but an inflorescence, and is called a **compound fruit.**

The wall of a true fruit may, when ripe, be dry (e. g. a nut), or fleshy (e. g. the cherry); in either case it is described as the **pericarp,** and represents the wall of the ovary. When the fruit is more than one-seeded and dry, it commonly splits when ripe so as to liberate

the seeds, and is then described as **dehiscent**; if no splitting takes place before the germination of the enclosed seed, or if the splitting is such as merely to divide the fruit into one-seeded portions without liberating the seeds, it is described as **indehiscent.**

Classification of Fruits.

(A.) Simple Dry Fruits.

(*a.*) Indehiscent.

The **achene** is a one-seeded fruit with a thin coriaceous pericarp, and is the product of a monocarpellary superior pistil. Simple fruits of this kind are rare, but achenes are common as aggregates (e. g. buttercup, rose, &c., Fig. 178, III, p. 357).

The **caryopsis**, the characteristic fruit of the grasses (e. g. wheat, barley, maize), is really a form of achene in which the testa of the seed cannot be separated from the pericarp. If a grain (fruit) of maize be examined it is easy to see, on one side, the scar left by the style, thus showing that the outer coat is the pericarp and not the seed-coat (testa), and that therefore the grain is a fruit and not a seed (Fig. 170, IX, p. 325).

The **cypsela** is the characteristic fruit of the *Compositæ* (Fig. 170, IV); it is much like the typical achene, from which it differs in being inferior and representing two carpels although it is only one-seeded. Such a fruit may be surmounted by a pappus supported on a long stalk, as in the dandelion (Fig. 172, III, p. 332). A similar fruit is found in the *Dipsaceæ*, and in the valerian and other *Valerianaceæ*; in the latter case it represents a tricarpellary ovary.

The **nut** differs from the typical achene in having a hard woody pericarp, in being inferior, and in representing more than one carpel. It is the characteristic fruit of many of the *Cupuliferæ* (e. g. hazel, oak, beech, &c.), in all of which the ovary is at first bilocular or trilocular, generally with one or two ovules in each loculus; all except one of the ovules are aborted during the development of the fruit. It should be remembered that many so-called nuts are not, botanically considered, nuts at all; the Brazil-nut and horse-chestnut are seeds, the shell being simply the testa; the cocoa-nut and almond are fibrous drupes (p. 322).

The **single samara** of the birch, alder, ash, &c., is practically an

achene with a winged pericarp to assist in the dispersal of the fruit and seed (Fig. 167, IV, V).

The **schizocarp** differs from the preceding forms in being two or more seeded, and in splitting into as many separate parts as there are seeds, but not so as to liberate the latter. The **double samara** of the maple and sycamore is a two-seeded, winged schizocarp (Fig. 167, II); the fruit of the geranium splits along the septa which

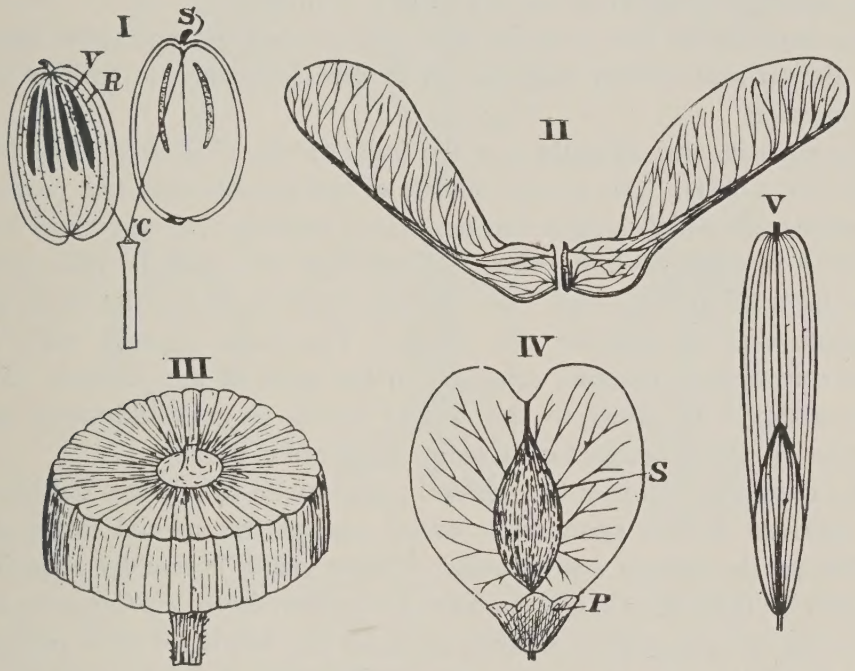


FIG. 167. Winged fruits and schizocarps. I. Fruit of the Cow-parsnip (*Heracleum*), one of the *Umbelliferæ*. A schizocarp. C=carpophore; R=ridges containing vascular bundles; S=style; V=oil receptacles (vittæ). II. Fruit of the Sycamore. A schizocarp or double samara. III. Schizocarp of the Marsh Mallow. The persistent calyx and epicalyx have been removed. The fruit splits into many one-seeded portions. IV. Samara or winged achene of the Elm. P=perianth; S=seed. V. Samara of the Ash. Two-seeded.

divide the carpels, into five one-seeded portions called **mericarps**—the whole is often called a **regma** (Fig. 182, V, p. 369); the **cremocarp** of the *Umbelliferæ* divides into two mericarps, which remain for some time attached to a **carpophore** (Fig. 167, I); the fruit of the mallow is termed a **carcerule**, and splits into many one-seeded portions or mericarps (Fig. 167, III); the **lomentum** of the radish or bird's-foot trefoil is a schizocarp, which splits transversely into one-seeded portions.

(*b.*) Dehiscent.

Dehiscent fruits are generally many-seeded.

The **follicle**, the fruit of the larkspur, represents a single superior carpel, and it splits along one suture only (generally the ventral one, i. e. the line of attachment of the infolded margins of the carpellary leaves along which the seeds are arranged). The follicle often occurs as an aggregate fruit (*Crassula*, Fig. 155, I, p. 291).

The **legume** is also superior and monocarpellary, but splits along both dorsal and ventral sutures. It is the characteristic fruit of the *Leguminosæ*.

The **siliqua** and **silicula** are the fruits of the *Cruciferæ* (Fig. 180, IV, V, VI, p. 361). The ovary consists of two carpels with two parietal placentæ from which a false septum arises, making the ovary and fruit bilocular instead of unilocular. When ripe the carpels split away from the false septum and from the placentæ to which the seeds are attached, and so liberate the latter. The false septum with its frame (or replum) remains attached to the apex of the pedicel. The name **siliqua** is given to the longer forms (e. g. wallflower), and **silicula** to short broad forms (e. g. shepherd's purse).

The **capsule**. This is the general name given to any dry dehiscent fruit derived from a syncarpous ovary, except the special forms described as the siliqua and silicula. The capsule is usually superior, but may be inferior as in *Campanula*, *Iris*, willow-herb (*Epilobium*), &c.

The dehiscence generally takes place by the formation of a number of longitudinal slits; if each carpel splits along its dorsal suture or midrib so that the chambers or loculi of the fruit are opened into, as in the violet, *Narcissus*, and *Iris*, the dehiscence is described as **loculicidal**; if in a multilocular fruit the carpels are separated by the splitting of the septa between them, as in *Hypericum*, the dehiscence is **septicidal**; if splitting takes place along the dorsal sutures and also across the septa so that the placentæ remain united into a central column, as in the thorn-apple, the dehiscence is **septifragal**.

The capsule may dehisce by the formation of teeth as in the *Caryophyllaceæ* (Fig. 181, V, p. 365); or by holes or pores formed by the removal of small portions of tissue in certain spots as in the poppy (Fig. 168, I); or the dehiscence may be by a transverse split which separates a lid from the upper part of the capsule as in the scarlet

pimpernel (*Anagallis*) and plantain (*Plantago*); this form of capsule is called a **pyxidium** (Fig. 168, VI). Although capsules are typically

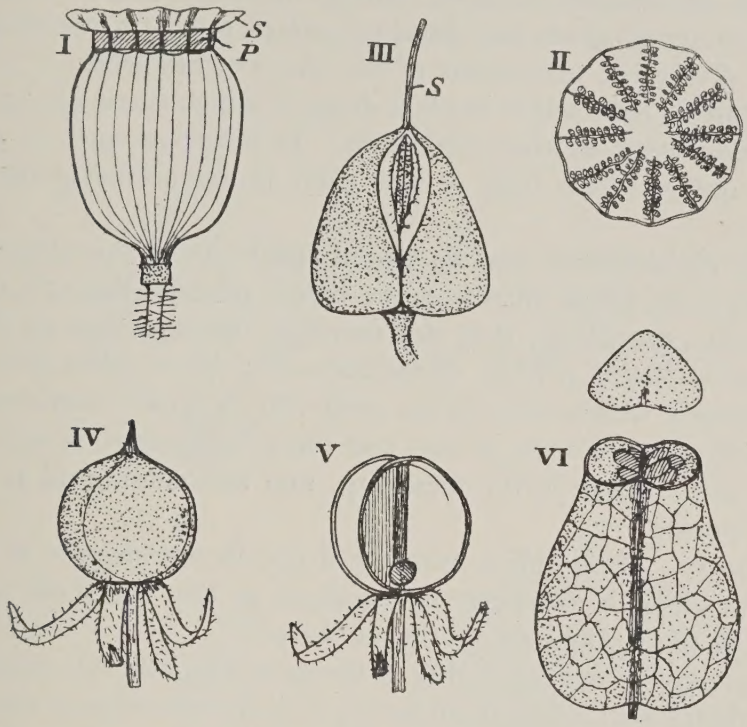


FIG. 168. Capsular fruits. I. Poppy. A porous capsule. P=pore; S=stigma. II. Transverse section of the same, showing the seeds attached to projecting placentæ which do not meet in the centre. III. Foxglove. A bilocular capsule which is just beginning to split open along the septa. S=style. IV. A trilocular capsule. V. The same after dehiscence. The outer part of each carpel has fallen off by splitting of the septa. VI. Henbane (*Hyoscyamus*). A bilocular capsule with transverse dehiscence. A pyxidium.

dry fruits, some, such as those of the balsam, dehisce and scatter their seeds while still in a green and more or less succulent condition.

(B.) SIMPLE SUCCULENT FRUITS.

These are indehiscent; the pericarp is frequently differentiated into layers, one of which is often dry and hard (sclerenchymatous) forming a 'stone' as in the common 'stone-fruits' (e.g. cherry, &c.).

The **drupe**. The typical fleshy drupe is the product of a monocarpellary superior ovary. The pericarp is differentiated into three layers, an outer thin skin or **epicarp**, a thicker juicy middle portion or flesh known as the **mesocarp**, and a hard stony portion which surrounds and protects the seed, the **endocarp**. Typical simple drupes are found

in a number of rosaceous plants, e.g. the cherry, peach, plum, damson (Fig. 184, IV, p. 374), &c. The walnut fruit is a drupe from which the mesocarp and epicarp separate during ripening, and in which the endocarp is two-valved, and develops partial septa on its inner side so as to divide the cotyledons of the embryo into lobes.

The fruit of the holly is really a drupe in which there are as many distinct endocarps as there are seeds. It is the product of a syncarpous ovary. The fruit of the elder is essentially of the same nature.

In this division may also be placed the fruits of the almond and cocoa-nut palm, which differ from the typical drupe in having a fibrous, not a fleshy, mesocarp; they are therefore distinguished as **fibrous drupes** (Fig. 184, V, p. 374). In the cocoa-nut the so-called shell is the hard endocarp within which is the seed with its brown testa and white endosperm; in the latter, at one end the small embryo is embedded. The cocoa-nut fibre is the mesocarp, and surrounding all is a thin smooth epicarp.

The berry. This differs from the drupe in the absence of a hard endocarp, which in the berry is succulent, so that the seeds are embedded in the fleshy part of the pericarp.

Berries may be one-seeded (e.g. the date, Fig. 169, III), few-seeded (e.g. barberry with one to three seeds), or many-seeded (e.g. cucumber, gooseberry, &c., Fig. 169, I, II). A berry may be the product of a single carpel (e.g. barberry); of two carpels with parietal placentæ (e.g. gooseberry), or with axile placentæ (e.g. bitter-sweet); or it may have several loculi representing the carpels, as in the orange (Fig. 169, IV). Berries may be superior, as in the orange, barberry, bitter-sweet, and grape; or inferior, as in the cucumber, melon, gooseberry, and currant. The succulent part of the fruit is often largely formed by the placentæ and seed-coats, as in the gooseberry. The berries of the *Cucurbitaceæ* (cucumber, melon, &c.) are often described by the special name of **pepo**.

The **hesperidium** is a special name given to the fruit of the orange, lemon, &c. It is superior and multilocular with axile placentæ; the outer orange-coloured skin is the epicarp, the underlying white portion is the mesocarp, and the thin membranes which surround the loculi and separate them from one another constitute the endocarp (Fig. 169, IV). The flesh of the orange in which the seeds are embedded consists of juicy hairs which grow out from the inner walls of the loculi.

The pome (Fig. 184, VI, p. 374). This name is given to the fruit

of the apple, pear, medlar, and hawthorn. Fruits of this kind are formed in those rosaceous plants which have the carpels fused with the receptacular tube so as to form an inferior spuriously syncarpous ovary (see p. 374). The true pericarp is here enclosed in the thick

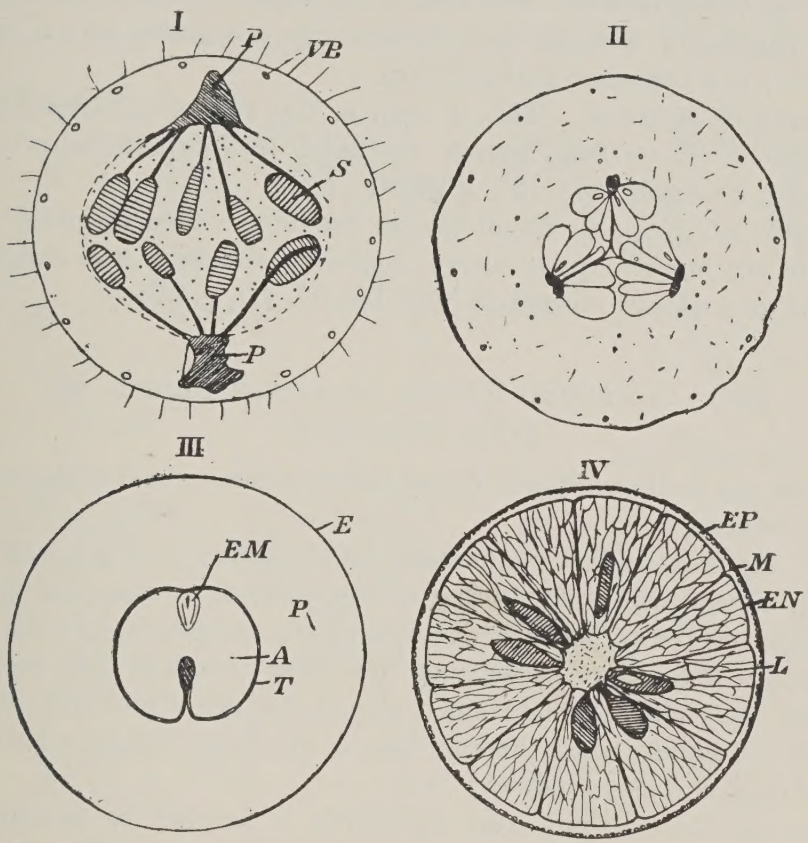


FIG. 169. Berries. I. Transverse section of Gooseberry fruit. P, P=placentæ; S=seeds; VB=vascular bundles. The central succulent portion is formed by the placentæ and seed-coats. II. Transverse section of fruit of Cucumber. A many-seeded inferior berry. Three placentæ. III. Transverse section of fruit of Date. A one-seeded berry. A=hard endosperm; E=thin epicarp; EM=embryo; P=fleshy part of pericarp; T=testa of seed. IV. Transverse section of an Orange fruit. A multilocular berry or hesperidium. EN=endocarp; EP=epicarp; L=one of the loculi filled with juicy hairs and containing seeds; M=mesocarp.

fleshy receptacle so that the whole is a pseudocarp. In the fruits of the apple and pear the pericarp is thin and coriaceous; in those of the hawthorn and medlar it is stony.

(C.) AGGREGATE FRUITS.

These are collections of fruits formed from the separate carpels of an apocarpous pistil; they are also known as **etærios.**

Etærio of achenes. Examples are *Ranunculus*, *Clematis*, *Potentilla*, and *Geum* (Fig. 184, VII, p. 374), in which the receptacle on which the fruits are inserted is dry, and the strawberry, in which the fruits are attached to a swollen fleshy receptacle, so that the whole is a pseudocarp (Fig. 184, I, p. 374). The fruit of the rose (the **hip** or **cynarrhodum**) consists of a fleshy receptacular cup containing an etærio of achenes ; it is therefore a **pseudocarp.**

Etærio of follicles. This is seen in the columbine (*Aquilegia*), monkshood (*Aconitum*), marsh marigold (*Caltha*), meadow-sweet (*Spiræa*), *Crassula* (Fig. 155, I, p. 291), &c.

Etærio of drupes. Small drupes are often called drupels. The fruits of the blackberry, dewberry, raspberry, &c., consist of etærios of drupels on a convex receptacle (Fig. 184, II, III, p. 374).

(D.) Compound Fruits, Multiple Fruits, or Infructescences.

These are fruits which are derived from inflorescences and not from single flowers.

The **fig fruit** is best understood by examining it in a young condition, when it will be found that a large number of unisexual flowers are borne on the surface of a deeply-concave receptacle. In the fruit, the fleshy outer part consists of the receptacle, and the so-called 'seeds' are really achenial fruits each one of which represents a female flower. [Compare with the rose-hip in which the achenes represent the carpels of a *single* flower.]

The **mulberry fruit** also represents a number of flowers, the perianth leaves of which persist and become fleshy.

The **pineapple** is somewhat similar, but the axis of the spike as well as the individual flowers become fleshy and fuse together. The individual fruits are really berries, which in a state of cultivation are seedless. The axis of the inflorescence grows beyond the fruit and forms a crown of leaves.

The fruit of the fig is technically described as a **syconus**; that of the pineapple or mulberry as a **sorosis.**

The fruit (**strobilus**) of the hop also represents an inflorescence ; the true fruits are concealed by the scaly bracts.

Some fruits already described may also be placed here, e. g. the fruits of *Compositæ*, *Dipsaceæ*, &c., if the whole collection of fruits formed from a head of flowers is considered and not a single fruitlet.

THE SEED.

It has been already pointed out that the production of seeds, each containing an embryo plant, is the most characteristic feature in the life-history of the phanerogams as distinguished from the cryptogams—

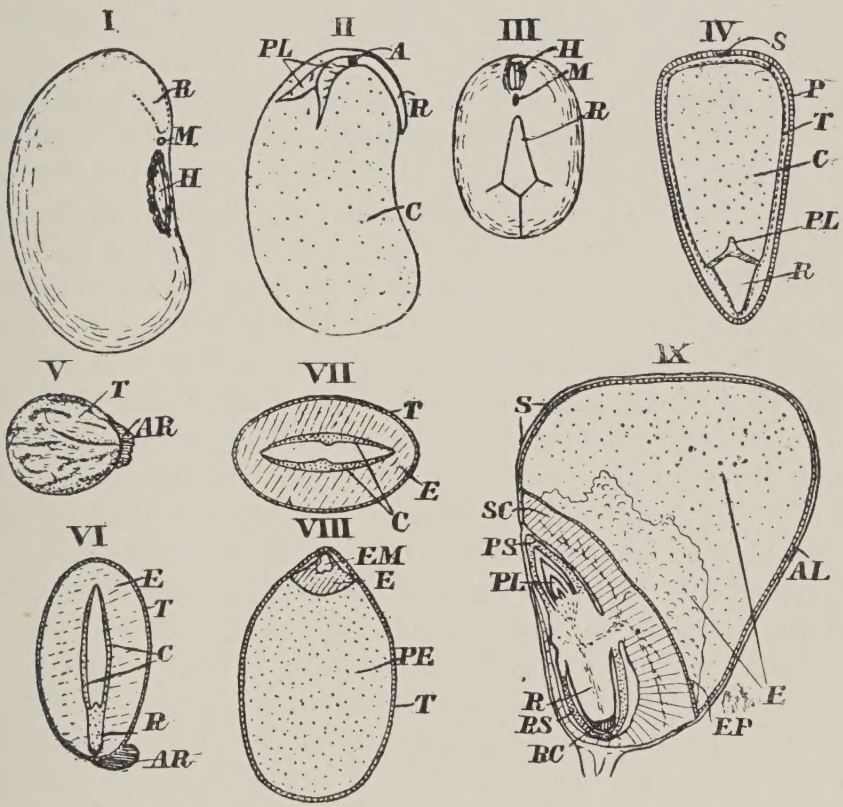


FIG. 170. Structure of seeds. I. Seed of Bean. II. Seed of Bean with the seed-coat and one cotyledon removed. III. Seed of Pea. The cotyledons and radicle can be seen through the testa. IV. Vertical section through a Sunflower fruit. V. Seed of the Castor-oil plant, showing the aril. VI. Vertical section of the same at right angles to the plane of the cotyledons. VII. The same in transverse section. VIII. Vertical section through a seed of a Water-lily (*Nuphar*), showing perisperm and endosperm. IX. Vertical section through a grain (fruit) of Wheat. A=place of attachment of detached cotyledon; AL=aleurone layer; AR=aril; C=cotyledon or cotyledons; E=endosperm; EM=embryo; EP=epidermis of scutellum; H=hilum; M=micropyle; P=pericarp; PE=perisperm; PL=plumule; PS=plumule sheath; R=radicle; RC=root-cap; RS=root-sheath; S=style; SC=scutellum; T=testa.

the former being essentially the **seed-bearing plants**, while the latter produce nothing morphologically comparable with a seed.

A seed is produced from an ovule as the result of fertilization of the oosphere, and the subsequent growth and differentiation of the oospore

into an embryo plant. This first growth and differentiation of the embryo, leading to the production of a seed, takes place while the embryo is still contained in the macrosporangium (ovule), and while attached to the parent sporophyte; the growth of the embryo is finally arrested, and the resting embryo so formed, together with what remains of the remainder of the ovule, constitutes the ripe seed, which afterwards becomes detached from the parent plant. Later on, under suitable conditions, growth recommences and the seed is said to germinate.

As an example of a seed we may study that of the bean-plant, which should be examined after soaking in water for some hours (see Fig. 170, I, II). The seed is exceptionally large. We may notice the dark-coloured scar or **hilum** marking the place of attachment to the short stalk or **funicle** of the seed, and at one end of this a small hole or **micropyle** easily observed if the soaked seed is squeezed so as to force out some of the water. If the **seed-coat** or **testa** is removed the **embryo** will be exposed, and will be seen to consist of two thick fleshy lobes or **cotyledons**, a small bud with leaves, easily made out with a lens, lying between the cotyledons, and known as the **plumule** or rudimentary shoot, and the **radicle** or young root with its free pointed end directed towards the micropyle in the seed-coat. The seed-coat or testa is generally derived from the *outer* integument only of the ovule, and the contained embryo is formed from the oospore, so that during the ripening of the seed the endosperm (prothallium) in the embryo-sac, as well as the nucellus tissue outside the embryo-sac, and the inner integument, all disappear, while the embryo increases enormously in size by the absorption of this and other food-material which is stored for future use in the cells of the cotyledons.

Let us now compare the seed of the bean-plant with that of the castor-oil plant (*Ricinus*) (Fig. 170, V, VI, VII). If we split off the hard brittle seed-coat of the latter, a second thin coat will be found derived from the *inner* integument of the ovule; this inner coat is not found in many ripe seeds. Within is a somewhat flattened mass of oily tissue which cannot be separated into two cotyledons as in the bean, but is really outside the embryo altogether, and represents the persistent **endosperm (prothallium)** of the embryo-sac (see p. 138). If we cut longitudinally through the mass of endosperm, it will be found to enclose a flattened central cavity, on the sides of which are the two thin flattened veined cotyledons, with the plumule and

radicle below. Comparing the two seeds we find the following important differences:—

(1) The seed-coat of the bean-plant encloses nothing but the embryo, while that of the castor-oil plant encloses a mass of endosperm tissue in addition to the embryo.

(2) The cotyledons of the bean seed are very thick and fleshy, as the food, which is necessary for the young plant when the seed germinates, is stored in their cells; the cotyledons of the castor-oil seed are thin, as the reserve food-material is not stored in them but in the cells of the endosperm.

Seeds, such as those of the bean-plant, in which no endosperm is present in the ripe condition owing to the absorption into the embryo of that formed after fertilization (see p. 138), are described as **exalbuminous**; those in which the endosperm persists as **albuminous**. In some seeds the amount of endosperm which persists until the seed is ripe is so small that it appears to be exalbuminous, e.g. the wallflower seed contains a single layer only of endosperm cells.

As another example of an exalbuminous seed the fruit and seed of the sunflower may be examined (Fig. 170, IV). If we dissect off the brittle pericarp we shall see the thin testa enclosing an embryo with two cotyledons, with a radicle directed towards the base of the fruit, and a very minute plumule lying between the two cotyledons. The flattened seeds of the cucumber and of honesty may also be examined.

As other examples of albuminous seeds and fruits we may examine those of the date and maize. Seeds of the date should be soaked in water for some days, and then cut transversely across the middle with a sharp knife; the small embryo will be seen towards the grooveless side of the seed; the hard tissue forming the greater part of the seed is thick-walled endosperm (see Fig. 169, III, p. 323).

The 'grains' of wheat, maize, &c., are really fruits (**caryopses**) characterized by the close adhesion of the testa to the pericarp, so that they cannot be readily separated (Fig. 170, IX). Let us examine a grain of maize and note the scar left by the style, the laterally-placed paler-coloured embryo, and the yellow endosperm. Also we may dissect off the outer coats of the grain, and afterwards dissect the embryo from the endosperm. If we cut longitudinal sections of some soaked grains so that they pass centrally through the embryo, we shall see the radicle and plumule, the former with its **root-sheath** or **coleorhiza**, and the latter with its **plumule-sheath** or **pileola**. On the side of the embryo towards the endosperm is a shield-like

portion of the embryo known as the **scutellum**, through which food-material is absorbed from the endosperm. The scutellum is by some considered to be the single cotyledon; others regard the first formed sheathing leaf (**pileola**) of the plumule as the cotyledon, and yet others regard a small ligular appendage on the opposite side of the embryo to the insertion of the scutellum as having that rank.

The albuminous seed of the lily should also be examined (cp. *Alisma*, Fig. 86, which has a somewhat similarly shaped embryo, but no endosperm).

The seeds of monocotyledons are typically albuminous; exceptions are found in many water forms (e. g. *Alisma*), and in the *Orchidaceæ*.

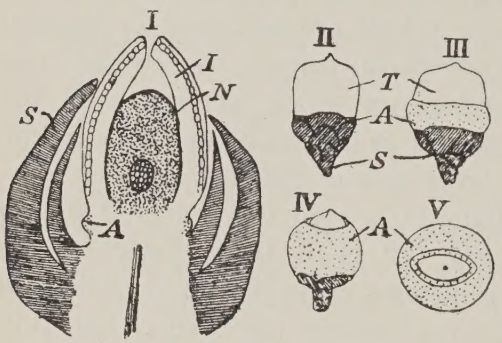


FIG. 171. Ovule and seed of the Yew (*Taxus baccata*), showing the development of the aril. I. Vertical section of end of branch with terminal ovule. A=rudiment of the aril, an outgrowth from the stalk or funicle; I = integument; N = nucellus; S=scaly leaves. II, III, IV. Successive stages in the development of the aril. A=aril; S=scaly leaves; T=testa of seed. V. Seed from above. A=aril.

The seeds of dicotyledons are typically exalbuminous, but exceptions are found in *Nymphæaceæ* (the water-lilies), *Umbelliferæ*, *Euphorbiaceæ* (e.g. *Ricinus*), &c.

In some few cases a portion of the nucellus persists and forms part of the ripe seed. It is known as **perisperm** in the seed, and it may occur either with or without endosperm. A good seed in which to see perisperm is that of the white water-lily (*Nymphæa*). After removing the hard seed-coat a longitudinal section of the enclosed mass will show a large mass of perisperm enclosing near one end a much smaller mass of endosperm, and that again the minute embryo (Fig. 170, VIII).

Some seeds show variously-formed outgrowths, or additional integuments, which are gradually developed as the seed ripens. These accessory growths are known as **arils**, and they may be developed from the funicle or stalk, from the hilum, or from the micropyle, and in this latter case is distinguished as an **arillode**. An example of a fleshy aril is seen in the yew (a gymnosperm), in which it takes the form of a red cup, which almost completely covers the seed; this cup gradually grows up from the funicle (Fig. 171). The water-lily (*Nymphæa*) has a somewhat similar cup-like aril. The spindle-tree

(*Euonymus*) has a bright scarlet, fleshy arillode. The seeds of the willow and of the poplar have an aril in the form of a tuft of hairs, also those of the willow-herb (*Epilobium*), Fig. 172, II, p. 332. The seed of the castor-oil plant also has an aril (Fig. 170, V).

(*a.*) The Germination of Seeds.

Given the required conditions as to moisture, temperature, presence of oxygen, &c., a seed begins to grow or germinate into a young plant or seedling. The mode of germination is not the same in all cases, and there is generally marked contrast between the germination of dicotyledonous and monocotyledonous seeds.

As an example of the former we may take some bean seeds, soak them in water for a few hours, and then allow them to germinate in moist sawdust. The imbibition of water first causes swelling of the seed, followed by cell-division and growth of the embryo, and as a result the radicle soon protrudes through the micropyle and begins to grow downward as the young root. A little later the plumule protrudes from the side of the seed and begins to grow upward as the young stem of the seedling. At the same time the stalks of the cotyledons elongate and become clearly visible, and their place of insertion on the stem serves to mark off the rapidly elongating **epicotyledonary** part of the stem above from the short **hypocotyledonary** stem between the cotyledons and the upper limit of the root. The primary root formed directly from the radicle continues to elongate and thicken so that it remains throughout the life of the plant as the main- or **tap-root**, on which secondary (or lateral) roots soon begin to arise in rows opposite to the xylem bundles in the main root (see pp. 12 and 70). All the roots bear root-hairs at some distance behind their growing points. Meanwhile the epicotyledonary portion of the stem elongates and develops its leaves, &c. The early growth of the plant is mainly at the expense of the reserve food-material which is stored in the cotyledons (see Part III, p. 447), which remain underground enclosed in the testa. As the food-materials are absorbed the cotyledons gradually shrivel up. When, as in the bean and pea, the cotyledons never appear above the ground as green leaves, the germination is described as **hypogeal.**

If we now germinate some seeds of mustard or cress or buckwheat, we shall see the tap-root, root-hairs, &c., as in the bean; we may note, however, that, owing to the elongation of the hypocotyledonary

stem the cotyledons are carried up into the air and become the first green leaves of the plant, i.e. the germination is epigeal. The same thing may also be seen in seedlings of maple or sycamore, which are readily found. In the buckwheat, which is an albuminous seed, the cotyledons remain for a considerable time enclosed in the seed, during which they absorb the endosperm. They are subsequently liberated.

The foregoing examples are all dicotyledons. We will now examine some monocotyledonous forms. Allow some barley grains to germinate in moist sawdust for a few days. It will be seen that there is no main- or tap-root, but a number of approximately equal roots, some of which arise from the undeveloped radicle and pierce the root-sheath (coleorhiza), while others arise a little higher up and from the stem, i.e. they are adventitious. As the plant grows, fresh roots are developed from the stem at successively higher levels, so that nearly all the roots are adventitious. The plumule grows up into the air, and bursts through the plumule sheath (pileola), which now forms a nearly colourless sheath surrounding the developing green leaves, &c.

Let us next germinate some maize grains and compare them with those of barley; the radicle here elongates and bursts through the end of the coleorhiza, which can be seen as a ring round the base of the young root. The radicle forms lateral roots, but, as the former never becomes thickened and as the adventitious roots which arise from the lower part of the stem soon equal and exceed the primary one in size, there is no tap-root. The adventitious roots continue to arise as the plant grows, many of them arising from quite high nodes of the stem, so that they form buttresses passing through the air to the soil. The plumule develops much as in barley. The outermost leaf of the plumule (the pileola) forms no green lamina.

Seedlings of the date should also be examined. The primary root elongates into a long thin organ, and the greater part of the cotyledon emerges from the seed and shows a distinct sheath and stalk. The tip of the cotyledon remains, however, enclosed in the seed and serves to absorb the food-materials stored in the endosperm (cp. the scutellum of grasses).

(*b.*) The Dispersal of Fruits and Seeds.

Plants exhibit many interesting adaptations which have for their object the scattering of the seeds over as wide an area as possible.

Abundant as some plants may be in certain localities, but little observation and reflection are needed in order to convince the student that only a very small proportion of the seeds produced during a certain season are represented by plants during the next. This is due to the struggle for existence between plants of the same species, as well as with other forms, so that few seeds are able to germinate, or even if they germinate, to come to maturity. The foxglove, for example, is an extremely common plant in some places, so common that every lane and hedgerow is lined with it ; and if we examine a single plant in early autumn, we shall observe that its long upright flowering stem bears perhaps as many as fifty or more capsules, each of which, on being shaken, will liberate a large number, approximately 1,000 or more, of black seeds. Suppose that all the seeds from one foxglove plant, perhaps 50,000 or more, were to fall immediately around the parent plant, how many would have any chance of germination? Possibly one or two would spring up next year if the soil and light were not monopolized by other plants, the rest would come to nothing. There may be, however, within a short distance, an area within which the struggle for existence is less keen, and it is obviously an advantage to the plant if some of its seeds could be carried there in some way or other, for the chance of survival would be greater.

Again, what chance is there of the survival of the seeds of a tree (e. g. a sycamore) if they fall within the stifling shade of the parent? They may germinate, for sycamore seedlings can often be found in great abundance; but how many come to maturity? But should they be carried away by the wind the seeds may find a place where there is less competition.

Dispersal by the wind. Many fruits and seeds are provided with arrangements by which their surface is increased, without proportionate increase in weight, so that they may be the more easily carried along in currents of air. Many forest trees (e. g. ash, *Ailanthus*, sycamore, elm, &c., Fig. 167, p. 319) have winged fruits, and others (e. g. the pine) have winged seeds (p. 164) ; such fruits are often rather heavy and are not likely to be carried great distances except by very strong winds—it is, however, something to be carried even a short distance from the parent tree.

Other fruits, such as those of the dandelion and other *Compositæ*, valerian, &c., have a pappus of hairs. Every one is familiar with the beautiful fruit of the dandelion with its delicate parachute-like pappus surmounting a long stalk—an excellent arrangement for dispersal

through the air (Fig. 172, III). *Clematis* has a somewhat similar arrangement, only here it is the persistent style that is hairy ('feathery,' Fig. 172, IV).

All the preceding instances, except *Pinus*, have been indehiscent fruits, but plants with dehiscent, capsular fruits sometimes have their seeds provided with hairy (**comose**) appendages, as in the willow, poplar, cotton-plant, willow-herb (*Epilobium*, Fig. 172, II), &c.

Sometimes seeds are so small and light that they are readily wafted through the air without special modifications such as wings, &c.

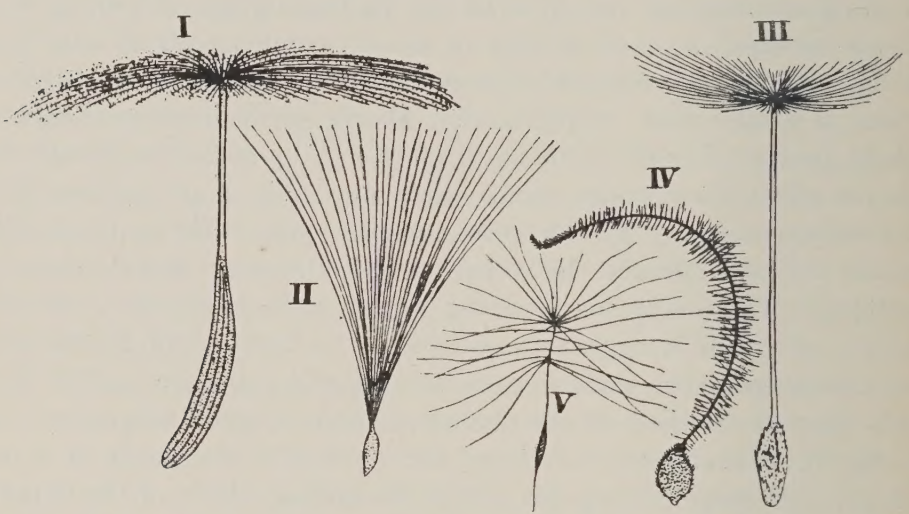


FIG. 172. Some fruits and seeds provided with arrangements for their dispersal by the wind. I. Achene of the Goat's-beard (*Tragopogon*), one of the *Compositæ*, with a long beak and feathery pappus. II. Seed of the Willow-herb (*Epilobium*). The tuft of hairs is an aril (see p. 329). III. Achene of the Dandelion, with a long beak surmounted by a pappus. IV. Achene of *Clematis* with a long persistent hairy style. V. Fruit of *Typha* ('bulrush').

Orchids have very small seeds in which the embryo is not differentiated into parts, radicle, plumule, &c.

Sometimes the arrangement and mode of dehiscence of the fruits are such that the seeds can be jerked out only during a strong wind, i. e. when the wind is sufficiently strong to carry the seeds to some distance. An arrangement of this kind is seen in the porous capsule of the poppy (Fig. 168, I), and in the fruits which are capsules dehiscing by teeth, of the *Caryophyllaceæ* (Fig. 181, V, p. 365).

Fruits with Explosive Mechanism. These are fruits which dehisce suddenly and with violence, so as to project the contained seeds to a considerable distance.

An example is seen in the touch-me-not (*Impatiens Noli-me-tangere*),

a species of balsam. The fruit is a succulent capsule, and when ripe the least touch causes the valves suddenly to separate and coil upwards, so shooting out the seeds. The fruits of the wood-sorrel (*Oxalis*) behave in much the same way, also those of the squirting cucumber (*Ecballium*).

The fruits of some leguminous plants (e. g. furze, &c.) also dehisce suddenly, and doubtless project the seeds to some distance; if one stands near a number of furze-bushes on a sunny day in the late summer, the clicking sound caused by the sudden dehiscence of the legumes can be heard easily.

Dispersal by Water. This is important in the case of aquatic plants such as the water-lilies, the seeds of which possess air-chambers to enable them to float on the surface of the water. Seeds may also be carried down by rivers and occasionally tossed up and deposited on the banks.

The fruits and seeds of some plants may be carried across the sea from island to island, or even to greater distances. Many seeds are rapidly killed by immersion in salt water, but others are able to resist its action for a long time: the experiments of Darwin showed that hazel-nuts will germinate after immersion in sea-water for ninety days, and asparagus after eighty-five days. It is said that some seeds will germinate after traversing the width of the Atlantic from America to Europe. The cocoa-nut palm is commonly distributed from one island to another by the flotation of its fruits across the sea; the smooth, thin epicarp keeps the water out, the fibrous air-containing mesocarp enables the fruit to float; and the seed is further protected from injury by the hard endocarp or shell.

Dispersal by Animals. This mode of dispersal is of great importance. The principal animals which are concerned in it are birds and mammals. Many succulent fruits, such as drupes and berries, are eaten by birds and other animals, and the seeds are ultimately ejected uninjured under the most favourable conditions for germination. The seeds are protected from injury while passing through the alimentary canal, either by a hard resistant testa, as in the seeds of berries, or by a hard endocarp, as in drupes. Seeds may even pass through the alimentary canals of more than one animal, e. g. horse, then bird, without undergoing injury. In this way heavy seeds are scattered far and wide. The number of seeds carried in this way must be enormous: Mr. Tegetmeier found something like 8,000 seeds in the crop of a single wood-pigeon. Migratory birds carry

seeds far from their native place; it has been found that a large number of the plants belonging to oceanic islands are such as have fruits or seeds capable of being carried by birds. Birds also carry seeds in other ways: the sticky berries of the mistletoe adhere to them, and are carried to the branches of trees where they may germinate; the hard part of the fruit, including the seed, may be dropped after the soft part has been pecked off; and seeds may be carried in mud attached to their feet, &c. Many fruits are provided with hooks by which they become attached to passing animals: burdock, with its hooked and spinous involucral leaves (Fig. 173, II), is a good example of this; the agrimony (*Rosaceæ*) also forms small burrs consisting of a cup-like receptacle provided with hooked hairs and containing two achenial fruits (Fig. 173, I); galium (*Rubiaceæ*, Fig. 191, III, p. 398) and the hound's-tongue (*Boraginaceæ*) also have burr-like fruits. An interesting case is that of geum (one of the *Rosaceæ*, see Fig. 184, VII, p. 374), in which the achenes are provided with long persistent hooked styles.

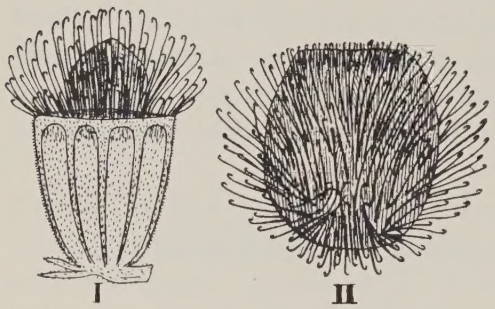


FIG. 173. Fruits adapted for dispersal by animals. I. Agrimony (*Rosaceæ*). II. Burdock (*Compositæ*).

Hooks and spines sometimes have also a protective function by preventing the fruits from being eaten by animals, which would otherwise destroy the seeds.

CHAPTER XX

OUTLINES OF CLASSIFICATION OF ANGIOSPERMS

IT is estimated that there are about 100,000 distinct kinds or species of angiosperms at present known to be living on the earth's surface. In order to study this enormous mass of material in an advantageous and scientific manner, it is necessary to classify the different forms, i. e. to arrange the plants in a number of groups, all the members

of one group agreeing in one or more characters. Thus we might divide plants into those with red flowers, those with yellow flowers, those with blue flowers, &c. But in selecting a character or characters on which our classification is to be based, it is obviously necessary to select such as are known to be constant in the flowers of an individual plant and in plants which agree with one another in most other characters. It follows from this requirement that a classification based on the colour of the flower would be unsatisfactory: (1) because the blossoms on an individual plant may vary in colour; (2) because the flowers produced from seeds formed in the same fruit may vary in the same way; and (3) because plants which agree with one another in all other respects may differ from one another more or less in but one character, and that the colour of the flower.

Colour, therefore, is in many cases such a highly variable character as to be quite unsuitable as a basis of classification, and such would result in bringing together plants which, while agreeing in the colour of the petals, are totally unlike in every other respect. The main object kept in view in our modern classification is not that of merely indexing plants without any regard for their real affinities, but is to arrange the plants first of all into small groups, the plants in each group agreeing with one another not only in one character but in most of their characters, and especially in those that are least variable. Could this be done perfectly each group would contain the plants which are most nearly *related* to one another, and which may be conceived, on the theory of evolution, to have all come from a common ancestor, i. e. they are *genetically* related to one another. It follows that the groups so made may be regarded as **natural** ones, in contradistinction to the artificial ones based on any one, or at most a few, characters.

The best known scheme of **artificial classification** is that due to Linnæus, the great Swedish naturalist of the eighteenth century, who placed all the flowering plants then known into twenty-three classes, founded on the number and arrangement of the stamens. Thus his **Monandria** included all plants with flowers which had a single stamen, his **Diandria** had two stamens, **Triandria** three stamens, and so on; while his **Didynamia** and **Tetradynamia** were distinguished by the relative proportion of the stamens as well as by their number. These classes were then subdivided according to the number of 'pistils' (i. e. carpels) into the orders **Monogynia**, **Digynia**, &c.

The **natural system of classification** has had a slow growth, and is not now and never will be in a perfect condition because the data which are necessary for the construction of a perfectly natural system of classification, are only partially known, and must remain so until a great deal is discovered about all the plants that are now living or have lived in all past geological ages. Linnæus himself clearly saw that the ultimate aim of the botanist must be a natural classification, but the system which is adopted at the present time is mainly due to two Frenchmen, Jussieu and De Candolle.

Adopting the Linnæan system of naming, every plant is given two names, the first the name of the **genus**, and the second that of the **species**. Thus the botanical name of the **marsh marigold** is *Caltha palustris*, the specific name *palustris* referring to the marshy habitat of the plant. The marsh marigold is described as a species of the genus *Caltha*. What, then, is the significance of this term *species*? Why do we say that all the specimens of *Caltha* found in Britain are of the same species, while specimens of *Viola* (the violet) have to be referred to several different species all included in the one genus *Viola*? Specimens of *Caltha* certainly vary among themselves considerably in the size of the flowers and other minor details, but the variations are such as are to be found in the plants produced from seeds contained in one fruit, and the predominance of *constant characters* leads to the belief that all the forms are descended from a common ancestor. Moreover, the pollen produced in one *Caltha* plant serves to fertilize the ovules of any other.

Now comparing the different violets with one another we find that while they all agree in many important respects, such as the number of parts and zygomorphism of the flower, nectaries growing from two of the anthers, parietal placentation, stipulate leaves, &c., they differ among themselves in several other characters, such as the size of the stipules, hairiness of the leaves, form of the stigma, colour and size of the flowers, &c., and, moreover, that these differences are such that they may be grouped into a few more or less distinct **forms** or **species**, the forms in each of which still exhibit variation, but in a less degree than that between the different species.

However, it is often extremely difficult to split up an assemblage of forms into good species, simply because they are in many cases connected by innumerable intermediate forms, as we should expect to be the case on the theory of descent with modification. As we believe that plant-forms are continually undergoing modification

or evolution, and that the plants of the present are but the altered descendants of those of the past, we must not expect to find sharply-demarcated species in all cases, and the wonder is that distinct forms can be recognized at all.

Some species show variation in a number of more or less definite directions, so that the variations may be classified into **sub-species** or **varieties**. Thus the marsh marigold shows three more or less constant British varieties, the commonest of which, with large flowers and spreading carpels, may be distinguished as *Caltha palustris*, var. *vulgaris*.

Latin is generally used for naming plants, the first or generic name being put in the substantive form, and the second or specific name in the adjectival form. As many plants have received different names by different botanists at various times, it is usual in systematic work to add to the name of the plant an understood abbreviation of the name of the botanist who is responsible for its specific name; e. g. *Caltha palustris*, Linn., indicates that Linnæus gave the name to the plant in question, and that we are referring to the plant to which Linnæus gave this name, and not to any other plant to which the same name may have been applied by another authority.

A number of allied species are grouped together into one **genus**, the limits of which are no more clearly defined than those of the species. The forms or species in a genus resemble one another more closely than they do the species of any other genus, and as in the species so in the genus, all the forms may be regarded as descended from one common stock, but the common ancestry is more remote in the case of the genus than it is in that of the species. Just as a species is sometimes conveniently divided into varieties, so the larger genera may be divided into **sub-genera**.

Proceeding to the next higher division, we come to the **order**, which is made up of several, sometimes of only one, genera. These are commonly described as **natural orders** in contradistinction to the old artificial orders of Linnæus. **Sub-orders** are also recognized.

A number of orders or families form a **cohort**: thus the **Cohort Ranales** with indefinite stamens, apocarpous pistil, &c., includes the natural orders *Ranunculaceæ* (buttercups, &c.), *Magnoliaceæ* (magnolias, &c.), *Nymphæaceæ* (water-lilies, &c.), &c. The cohorts are grouped into **series**, Thalamifloræ, Calycifloræ, and Gamopetalæ (pp. 340, 341, 342); and these again into the **sub-classes**, Dichlamydeæ and Incompletæ, according as the flowers are usually complete or

incomplete (p. 484), Spadicifloræ, &c. Finally, the sub-classes are grouped into the classes, Monocotyledons and Dicotyledons, by characters that are already known.

To take an example, the **water-cress** belongs to the—

Species: *officinale.*
Genus: *Nasturtium.*
Order: *Cruciferæ.*
Cohort: *Parietales.*
Series: *Thalamifloræ.*
Sub-Class: *Dichlamydeæ.*
Class: *Dicotyledons.*

The following is a table of the principal British Natural Orders arranged in series, sub-classes, &c., with the characters by which they are usually distinguished from one another, and references to the pages where the orders are described in more detail. It must be remembered, however, that while most common plants can readily be referred to their orders by using a table of this kind, exceptional plants may present great difficulty by their not agreeing in all the characters given for any order; e. g. *Nigella* is an exception to the rule that plants which belong to the *Ranunculaceæ* have apocarpous pistils. Moreover, some orders are much more clearly defined than others, and are therefore much more easily determined; e. g. most of the forms in the *Cruciferæ* are readily referred to that order by the constant occurrence of similar parts in the flower, while the plants belonging to the *Geraniaceæ* differ from one another in so many respects that the assemblage of forms is often broken up into several distinct orders.

In any case the table is to be regarded only as a key, and every plant should be compared with the fuller characters of the orders given in chapters XXI and XXII.

(A.) Class Monocotyledons.

I. Sub-Class Spadicifloræ.

The flowers are generally unisexual, sometimes dicœcious, and the inflorescence is usually a spadix with a spathe. Flowers rarely solitary. Perianth absent or rudimentary; never petaloid. Ovary superior.

* Order 1. **Araceæ**[1]. Large spathe and spadix; succulent fruits. Ex. *Arum* ('**lords and ladies**'). P. 344.

[1] Orders marked with a single star are not required for the Advanced Stage

* Order 2. **Typhaceæ.** Absence of a spathe; dry fruit. Ex. *Typha* (reed-mace or 'bulrush'). P. 345.

II. Sub-Class Glumifloræ.

Flowers hermaphrodite, or unisexual and monœcious, invested by stiff dry bracts or glumes; perianth absent or represented by scales or bristles; ovary superior and (in the British orders) unilocular, with one erect ovule; seeds with endosperm.

** Order 3. **Graminaceæ.** Leaves in two rows on the stem; hollow internodes; leaf-sheath split longitudinally on the side opposite to the lamina. P. 346.

* Order 4. **Cyperaceæ.** Leaves in three rows on the stem; stems generally three-angled, with solid internodes; leaf-bases sheathing but not split. Ex. *Cyperus*. P. 348.

III. Sub-Class Petaloideæ.

Flowers generally hermaphrodite, with two (sometimes one) whorls of three perianth leaves; perianth generally petaloid, but sometimes one or both series is herbaceous or scaly; ovary superior or inferior, generally syncarpous.

* Order 5. **Alismaceæ.** Perianth with a sepaloid calyx and petaloid corolla; ovary superior and apocarpous or nearly apocarpous. Marsh and water plants. Ex. *Alisma* (**water-plantain**). P. 349.

* Order 6. **Butomaceæ.** Like *Alismaceæ*, but with numerous ovules scattered over the walls of the carpels, which are six in number and in two whorls. Ex. *Butomus* (**flowering rush**). P. 349.

** Order 7. **Liliaceæ.** Six-leaved or six-lobed petaloid perianth; six stamens; trilocular superior syncarpous ovary; axile placentation. Floral formula (generally), P 3 + 3, A 3 + 3, $G\underline{(3)}$. Ex. **lily**. P. 350.

** Order 8. **Orchidaceæ.** Peculiar flowers; perianth very irregular; filament of the single stamen adherent to the style forming the column in the centre of the flower. Floral formula (generally), P 3 + 3, A 1, $G\overline{(3)}$. P. 352.

Order 9. **Amaryllidaceæ.** Perianth petaloid; six stamens; trilo-

Examination of the Board of Education, while those required for the Intermediate Scientific B.Sc. are indicated by a double star.

cular inferior ovary; axile placentation. Floral formula, P 3+3, A 3+3, $G\overline{(3)}$. Ex. *Narcissus*. P. 354.

Order 10. **Iridaceæ.** Perianth petaloid; three stamens; trilocular inferior ovary; axile placentation. Floral formula, P 3+3, A 3+0, $G\overline{(3)}$. Ex. *Iris*. P. 355.

(B.) Class Dicotyledons.

I. Sub-Class Dichlamydeæ. Series A. Thalamifloræ.

Sepals either free or coherent; petals generally free, rarely absent (some *Ranunculaceæ*); petals and stamens hypogynous; gynæcium apocarpous or syncarpous, ovary superior.

** Order 1. **Ranunculaceæ.** Numerous free hypogynous stamens and apocarpous gynæcium. Ex. *Ranunculus* (**buttercup**). P. 356.

* Order 2. **Berberidaceæ.** Calyx, corolla, and androecium generally trimerous; valvular dehiscence of anthers; one carpel. Ex. *Berberis* (**barberry**). P. 358.

* Order 3. **Nymphæaceæ.** Aquatics with floating leaves; indefinite petals and stamens; inner petals gradually passing into the outer stamens. Ex. *Nymphæa* (**white water-lily**). P. 359.

* Order 4. **Papaveraceæ.** Regular flowers with two sepals, four petals, indefinite stamens, syncarpous ovary, and parietal placentation. The sepals are caducous. Floral formula, K 2, C 2+2, A ∞, $G\underline{(2)—(\infty)}$. Ex. *Papaver* (**poppy**). P. 359.

** Order 5. **Cruciferæ.** Four sepals and petals (cruciform); tetradynamous stamens; characteristic ovary and fruit (siliqua or silicula). Floral formula, K 2+2, C×4, A $2+2^2$, $G\underline{(2)}$. Ex. *Cheiranthus* (**wallflower**). P. 360.

Order 6. **Violaceæ.** Flowers spurred; connectives of the stamens extended above the anthers; anthers slightly syngenesious; ovary with three parietal placentæ. Floral formula, K 5, C 5, A 5, $G\underline{(3)}$. Ex. *Viola* (**violet**). P. 363.

** Order 7. **Caryophyllaceæ.** Opposite entire leaves; cymose inflorescence; regular flowers; definite stamens; free central placentation. Ex. *Cerastium* (**chickweed**). P. 364.

* Order 8. **Hypericaceæ.** Opposite leaves often with pellucid glands; flowers regular; stamens in three or five bundles (polyadelphous). Floral formula, K 5, C 5, A (3–5)×∞, $G\underline{(3—5)}$. Ex. *Hypericum* (**St. John's wort**). P. 366.

Order 9. **Malvaceæ.** Regular flowers with valvate sepals and twisted petals; stamens monadelphous; characteristic ovary and fruit. [For *Tilia* (lime-tree), see p. 367.] Floral formula, K (5), C 5, A $(5 \times \infty)$, G$\underline{(\infty)}$. Ex. *Malva* (**mallow**). P. 367.

Order 10. **Geraniaceæ.** Flowers regular or irregular (spurred), pentamerous; stamens definite, often monadelphous; beak-like carpophore; free styles; characteristic fruit. [See *Impatiens* (balsam), *Tropæolum*, &c., p. 370.] Floral formula of **geranium**, K 5, C 5, A $(5+5)$, G$\underline{(5)}$. P. 368.

* Order 11. **Aceraceæ.** Opposite palmate leaves; fruit a samara. Ex. *Acer* (**maple** and **sycamore**). P. 370.

SERIES B. CALYCIFLORÆ.

Sepals generally coherent; petals generally free; petals and stamens perigynous or epigynous.

** Order 12. **Rosaceæ.** Leaves stipulate; flowers regular; stamens generally indefinite and perigynous; gynæcium apocarpous (sometimes spuriously syncarpous, e. g. apple). Odd sepal posterior. Ex. *Rosa* (**rose**). P. 371.

** Order 13. **Leguminosæ** (*Papilionaceæ*). Flowers papilionaceous; ten stamens, monadelphous or diadelphous; one carpel; characteristic fruit (legume). Odd sepal anterior. Ex. *Lathyrus* (**wild pea**). P. 376.

Order 14. **Saxifragaceæ.** Leaves exstipulate; flowers perigynous or epigynous; stamens definite; ovary syncarpous, but often free above; styles free. Ex. *Saxifraga* (**saxifrage**) with a superior ovary, and *Ribes* (**currant** and **gooseberry**) with an inferior ovary. P. 378.

Order 15. **Crassulaceæ.** Leaves fleshy; flowers regular; gynæcium apocarpous of as many carpels as there are sepals and petals. Ex. *Sedum* (**stonecrop**). P. 380.

Order 16. **Onagraceæ.** Flowers regular, tetramerous or dimerous; ovary inferior. Ex. *Epilobium* (**willow-herb**). P. 380.

* Order 17. **Cucurbitaceæ.** Flowers unisexual, monœcious or diœcious; characteristic foliage and tendrils; ovary inferior. Ex. *Bryonia* (**white bryony**). P. 381.

** Order 18. **Umbelliferæ.** Much-divided leaves with sheathing bases; flowers in umbels; flowers pentamerous, with an inferior ovary; characteristic fruit. Floral formula, K 5, C 5, A 5, G$\overline{(2)}$. Ex. *Æthusa* (**fool's parsley**). P. 382.

Series C. Gamopetalæ.

Calyx generally gamosepalous; corolla gamopetalous; stamens generally epipetalous, but free from the corolla in *Ericaceæ* and *Campanulaceæ*.

Order 19. **Ericaceæ.** Shrubby habit; stamens usually twice as many as the lobes of the corolla; anthers with appendages and dehiscing by pores. Ex. *Erica* (**heath**). P. 385.

** Order 20. **Primulaceæ.** Stamens opposite to the corolla lobes; single style and stigma; free central placentation. Ex. *Primula* (**primrose**). Floral formula (generally), K (5), [C (5), A 5], G$\underline{(5)}$. P. 387.

* Order 21. **Gentianaceæ.** Regular pentamerous flowers; petals contorted in the bud; ovary bicarpellary, with parietal placentæ. Floral formula (generally), K (5), [C (5), A 5], G$\underline{(2)}$. Ex. *Gentiana* (**gentian**). P. 388.

Order 22. **Oleaceæ.** Leaves opposite; flowers tetramerous, with two stamens. Ex. *Ligustrum* (**privet**). P. 388.

* Order 23. **Convolvulaceæ.** Climbing plants; sepals free; petals contorted in the bud; ovary bilocular, with two ovules in each loculus. Floral formula of *Convolvulus*, K 5, [C (5), A 5], G$\underline{(2)}$. P. 389.

Order 24. **Solanaceæ.** Regular pentamerous flowers; ovary bilocular and superior, with many ovules on axile placentæ; anthers sometimes syngenesious and dehiscing by pores. Floral formula, K (5), [C (5), A 5], G$\underline{(2)}$. Ex. *Solanum*. P. 389.

Order 25. **Boraginaceæ.** Leaves alternate; flowers pentamerous and regular; stamens five; fruit of four nutlets (as in *Labiatæ*). Plants often rough and hairy. Floral formula, K (5), [C (5), A 5], G$\underline{(2)}$. Ex. *Symphytum* (**comfrey**). P. 390.

** Order 26. **Scrophulariaceæ.** Flowers zygomorphic; stamens didynamous; ovary bilocular, with many ovules on axile placentæ. Typical floral formula, K (5), [C (5), A 4], G$\underline{(2)}$. Ex. *Digitalis* (**foxglove**). P. 392.

Order 27. **Plantaginaceæ.** Inflorescence a spike; flowers tetramerous, with scarious corolla; fruit a capsule. Floral formula (generally), K 4, [C (4), A 4], G$\underline{(2)}$. Ex. *Plantago* (**plantain**). P. 394.

** Order 28. **Labiatæ.** Square stems and opposite leaves; flowers lipped (bilabiate); stamens didynamous, as in *Scrophulariaceæ*;

fruit of four nutlets, as in *Boraginaceæ*. Floral formula (generally), K (5), [C (5), A 4], $G\underline{(2)}$. Ex. *Lamium* (**dead-nettle**). P. 394.

Order 29. **Campanulaceæ.** Flowers pentamerous; stamens free from the corolla; anthers with longitudinal dehiscence; ovary inferior, with many ovules. The plants generally have a milky latex. Floral formula, K (5), C (5), A 5, $G\overline{(2-5)}$. Ex. *Campanula*. P. 397.

* Order 30. **Rubiaceæ.** Leaves in whorls; flowers small, tetramerous or pentamerous. Ex. *Galium* (**cleavers**). P. 398.

Order 31. **Caprifoliaceæ.** Leaves opposite and exstipulate; flowers pentamerous, with epipetalous stamens; ovary inferior and generally multilocular. Floral formula, K (5), [C (5), A 5], $G\overline{(2-5)}$. Ex. *Lonicera* (**honeysuckle**). P. 399.

* Order 32. **Valerianaceæ.** Calyx inconspicuous; corolla spurred or saccate; stamens and carpels generally reduced to three, but only one carpel develops; inferior ovary and fruit one-seeded. Ex. *Centranthus* (**red valerian**). P. 400.

** Order 33. **Compositæ.** Flowers in capitula; stamens epipetalous; anthers syngenesious; ovary and fruit one-seeded. Floral formula, K pappus, 0 or (5), [C (5), A (5)], $G\overline{(2)}$. Ex. *Bellis* (**daisy**). P. 401.

II. Sub-Class Incompletæ.

Flowers monochlamydeous (i. e. with one perianth whorl only) or achlamydeous (i. e. without a perianth).

Order 34. **Urticaceæ.** Small green unisexual flowers; simple sepaloid perianth with stamens opposite to its lobes; fruit generally one-seeded. Ex. *Urtica* (**stinging-nettle**). P. 402.

Order 35. **Cupuliferæ.** Trees or shrubs with alternate leaves. Monœcious flowers generally in catkins; female flowers often surrounded by an investment of bracts which forms the cupule of the fruit. Ex. *Corylus* (**hazel**). P. 403.

** Order 36. **Salicaceæ.** As *Cupuliferæ*, but the flowers are diœcious, and the fruit is devoid of a cupule. Ex. *Salix* (**willow**). P. 406.

Order 37. **Euphorbiaceæ.** Herbs or shrubs (in British genera) with latex. Flowers unisexual; ovary usually trilocular, with one or two ovules in each cell; fruit usually dry and splitting into three cocci. Inflorescence a cyathium (in spurge, see p. 407). Ex. *Euphorbia* (**spurge**). P. 406.

Order 38. **Chenopodiaceæ.** Leaves exstipulate; flowers small and green in dense inflorescences; stamens opposite the segments of the perianth; ovary one-celled, with one ovule. Ex. *Chenopodium* (goosefoot). P. 407.

Order 39. **Polygonaceæ.** Leaves with ochreate stipules; ovary one-celled and generally triangular. Ex. *Polygonum* (**knotgrass**). P. 408.

CHAPTER XXI

THE MONOCOTYLEDONOUS ORDERS

I. Sub-Class Spadicifloræ.

* Order 1. **Araceæ.** The *Arum* family (Fig. 163, p. 301; Fig. 174, II, III). A large family; mainly inhabitants of tropical countries, where they sometimes occur as epiphytes of considerable size, clinging to trees by means of their aërial roots. The plants are generally herbaceous perennials, with a sympodial underground tuberous stem or rhizome; leaves alternate, often broad, petiolate, and net-veined like those of dicotyledons; flowers unisexual (monœcious) or hermaphrodite, and with or without a perianth; often very simple, sometimes reduced to a single stamen or a single carpel; fruit a berry.

The genus *Arum* belongs to the division of the order with unisexual naked flowers. The spathe is herbaceous and completely envelops the spadix in the young condition. The latter bears female flowers at its base, each consisting of a single carpel, and male flowers, each consisting of three or four coherent stamens higher up. Immediately above the fertile female flowers is a ring of sterile ones with long styles, and above the male flowers a ring of staminodes. The upper club-shaped part of the spadix is sterile and usually brightly coloured and attractive. *A. maculatum* ('**lords and ladies**') is the only British species (see also p. 301, Fig. 163).

The **sweet sedge** or **sweet flag** (*Acorus Calamus*) is the only other member of the order which occurs wild in Britain. It belongs to the division of the order with hermaphrodite flowers. The flowering shoot bears a terminal spadix, which, however, appears lateral, owing to

displacement by the spathe, which develops so as to form a continuation of the main axis (Fig. 174, II). Each flower has a perianth of six scales in two whorls, six stamens, and a two- or three-celled ovary with many ovules. Floral formula, P 3+3, A 3+3, G $\underline{(2-3)}$.

Well-known exotic plants belonging to this order are the **trumpet lily** (*Richardia æthiopica*); *Monstera*; the **flamingo-flower** (*Anthurium*), with a scarlet spathe and twisted spadix, &c.

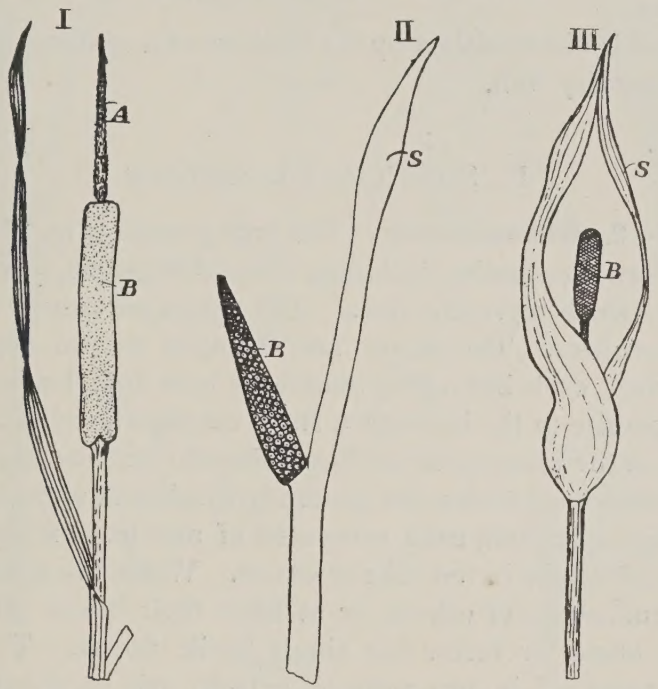


FIG. 174. *Spadicifloræ*. I. The Reed-mace or Bulrush (*Typha*), showing the long cylindrical spadix. A=part of spadix formerly occupied by male flowers; B=that occupied by female flowers, now represented by the closely packed fruits (see Fig. 172, V). There is no spathe. II. The Sweet Flag (*Acorus*). B=the terminal spadix, which appears lateral owing to displacement by the spathe; S=the spathe. The flowers are hermaphrodite. III. *Arum*, showing spathe (S). B=the upper sterile portion of the spadix.

The order is distinguished by the large spathe and spadix and by the succulent fruits.

* Order 2. **Typhaceæ.** The reed-mace family (Fig. 174, I). A small family, including the two British genera only, *Typha* (**reed-mace** or '**bulrush**') and *Sparganium* (**bur-reed**).

Aquatic or marsh plants with linear leaves and monœcious flowers on a long terminal spadix without a spathe in *Typha*, or in spherical spikes or heads in *Sparganium*. Perianth absent or represented by small scales; stamens either free or monadelphous; ovary generally of a single carpel with one ovule; fruit a small seed-like nut (see

Fig. 172, V, p. 332, for fruit of *Typha*). *Typha* has its flowers arranged on a long spadix, the lower, thicker part bearing only female flowers, and the upper only male. The perianth is replaced by long hairs forming a velvet-like pile covering the inflorescence. The stamens (1–5) are monadelphous. *Sparganium* has its flowers in spherical heads, the lower heads female only, and the upper smaller ones male. The perianth consists of a number of scales, and there are usually three free stamens.

The order is distinguished by the absence of a spathe, solitary ovule (usually), and dry fruit.

II. Sub-Class Glumifloræ.

** Order 3. **Graminaceæ.** The true grasses (Fig. 162). A very large and important order, including about 300 genera, of which about forty have British representatives. The plants are usually herbs, with hollow internodes. The leaves are arranged in two opposite rows (**distichous**); each has a long sheathing base split longitudinally on the side opposite to the lamina; a small outgrowth, called a **ligule**, is developed at the junction of leaf-base (**sheath**) and the lamina.

The inflorescence varies, but generally consists of variously grouped short spikes (spikelets), each composed of one (e. g. millet) or more flowers borne sessile in the axils of bracts. When the spikelet is one-flowered, rudiments of others, or at least their bracts (glumes), are developed above or below the single fertile flower. The spikelets are often arranged in two rows on a main axis, so forming a compound spike (e. g. wheat); or the main axis may branch, and these again, so as to form a kind of compound raceme, or, more correctly, spicate panicle (e. g. oat, Fig. 162, I, p. 300).

The individual flowers generally have the following structure (supra, p. 107): each arises in the axil of a bract known as the outer palea or flowering glume, opposite to which and at a slightly higher level, and so arranged that the two completely enclose the flower, is the inner glume or superior palea. Both these scales are situated below the flower, and within them are two very small scales, the lodicules, which are sometimes regarded as representing a perianth. These lodicules become larger and succulent at the time of flowering and so force apart the paleæ and glumes. The stamens are generally three in number (sometimes two whorls of three each, as in the bamboo, or there may be one or two stamens or a large number),

and have versatile anthers on weak filaments; the gynæcium consists of a single carpel, with generally two styles. [In most orders the number of styles and stigmas indicates the number of carpels in the pistil, but in grasses and a few other plants this is not so.] The fruit is a caryopsis (p. 325, Fig. 170, IX). No attempt can

FIG. 175. *Cyperaceæ*. I. Upper portion of a Sedge-plant, showing the inflorescences (spikes). II. Female flower of *Carex*. A=axis; B=bract; O=ovary surmounted by three large stigmas adapted for wind pollination; U=sheathing bract or utriculus (see VI). III. Male flower of *Carex*. B=bract enclosing three stamens. IV. Hermaphrodite flower of the Cotton-sedge (*Eriophorum*). B=bract. The perianth consists of hairs. V. Floral diagram of the Club-rush (*Scirpus*). The six perianth leaves indicated are bristly. VI. Diagram to illustrate the structure of the female flower of *Carex* (see II). B=bract, in the axil of which the axis S arises; O=ovary, which arises in the axil of the second bract; U=the second bract or utriculus.

be made in this work to deal with the British genera and species of grasses, for which a good flora, such as Hooker's 'British Flora,' should be consulted[1].

The *Graminaceæ* are distinguished from the *Cyperaceæ* by the two, not three, rows of leaves on the stem, by the hollow internodes, by

[1] Professor Marshall Ward's work on 'Grasses' (Cambridge University Press) may be recommended as a good illustrated account of this interesting family.

the split leaf-sheath, and by the, usually, monocarpellary gynæcium. Typical floral formula of the *Graminaceæ*, P 2 (?), A 3 + 0, G $\underline{1}$.

* Order 4. **Cyperaceæ.** The sedge family (Fig. 175). A large order of grass-like plants, comprising about sixty genera, of which seven are represented in Britain. The single genus *Carex* contains nearly fifty British species. They particularly affect moist situations.

The stems are often three-angled, with solid internodes. The leaves are in three rows (**tristichous**), and have sheathing bases ; the sheaths form closed tubes round the stem, not split ones, as in grasses.

The flowers are collected into spikes (or spikelets, Fig. 175, I), and each flower arises in the axil of a scaly bract or glume. The spikelets arise in the axils of scale-like or leafy outer bracts. The flowers are unisexual, as in *Carex* (Fig. 175, II, III, VI), or hermaphrodite, as in *Cyperus* and the cotton-sedge (Fig. 175, IV) ; the perianth is either absent or represented by a few bristles or scales ; stamens generally three ; gynæcium generally tricarpellary, sometimes bicarpellary, with a unilocular ovary and branching stigma ; fruit a caryopsis, often three-angled.

Among the genera with hermaphrodite flowers are :—

Cyperus, with flattened spikelets, bearing glumes or bracts arranged in two opposite rows and each containing a flower.

Scirpus, the club-rush (including the true bulrush), has its glumes on all sides of the spike. There is a bristly perianth (Fig. 175, V).

Eriophorum (the cotton-sedge or 'cotton-grass') has a hairy perianth, the hairs of which grow to a considerable length after flowering. It is common on damp moors (Fig. 175, IV).

Among the genera with unisexual flowers is :—

Carex, with the glumes imbricated all round the axis. The male flower consists of three stamens in the axil of a scaly bract (Fig. 175, III). Each female flower is borne on a short axis which arises in the axil of the bract (Fig. 175, II, VI, B) ; this short axis bears a leaf known as the 'second bract' or **utriculus**, in the axil of which the flower really arises. The utriculus forms a two-toothed tubular investment to the flower and fruit, and is sometimes regarded as a perianth. Some species of *Carex* are dicœcious.

The order is distinguished from the Graminaceæ by the triangular stems with solid internodes ; tristichous leaves, with the bases not split ; and the absence of a palea (inner glume) between the flower and the axis of the spikelet. Floral formula of *Carex*, ♂ (male) P 0, A 3, G 0; ♀ (female) P 0, A 0, G $\underline{(3 \text{ or } 2)}$. *Scirpus*, P (bristles), A 3, G $\underline{(3 \text{ or } 2)}$.

III. Sub-Class Petaloideæ.

A. Ovary superior.

* Order 5. **Alismaceæ.** The water-plantain family. A small family of marsh and water plants with a green calyx, petaloid (white or violet) corolla, two, six or a large number of stamens, and six or a large number of carpels forming a superior, apocarpous, sometimes partly syncarpous, pistil; ovules one or two in each carpel.

The **water-plantain** (*Alisma*) has radicle leaves and a flower stem with whorled branches forming a panicle. The three petals are delicate and deciduous; the six stamens are formed by the branching of three; carpels numerous in a single whorl (Fig. 176, I).

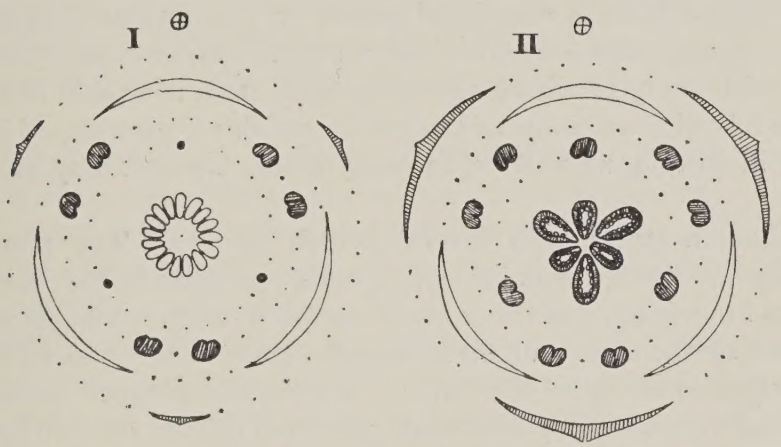


Fig. 176. Floral diagrams of *Alisma* (I) and *Butomus* (II).

The **common arrowhead** (*Sagittaria*) has arrow-shaped leaves, and monœcious flowers with numerous stamens and carpels.

The **star-fruit** (*Damasonium*) has six stamens and carpels, the latter cohering at the base and each containing two ovules.

The flowers in this order are sometimes monœcious, the seeds are without endosperm, and the floral formula is K 3, C 3, A 3^2+0 or ∞, $G\underline{^{6 \text{ or } \infty}}$.

* Order 6. **Butomaceæ.** The flowering rush family. A small family closely related to the *Alismaceæ*, and distinguished from that order by the possession of numerous ovules scattered over the walls of the carpels.

The **flowering rush** (*Butomus umbellatus*) has handsome flowers arranged in an umbellate cyme at the apex of a tall scape springing

from an underground rhizome. The flowers have a perianth of six leaves; nine stamens in two whorls, the outer whorl of six being formed by duplication of three; carpels six. Floral formula, K 3, C 3, A 3^2+3, $G^{\underline{3+3}}$ (Fig. 176, II).

** Order 7. **Liliaceæ.** The lily family. A large and important family occurring nearly all over the globe, divided into about 200 genera, of which eighteen have British representatives.

The plants are generally bulbous or rhizomatic herbs, but some exotic forms (*Dracæna* and *Yucca*) are arborescent, and increase in thickness by the formation of an extrafascicular meristematic zone in the pericycle (supra, p. 117). The **butcher's broom** (*Ruscus*) and *Smilax* are shrubs.

The flowers are usually hermaphrodite; they have a perianth of two similar alternating series, either gamo- or polyphyllous; six epiphyllous or hypogynous stamens; and a superior three-celled syncarpous ovary with many ovules on axile placentæ; fruit, a capsule or berry.

The following are some of the genera which are represented by wild forms in Britain, as well as, in many cases, having many cultivated ones:—

Allium, a genus with several British species. The plants are bulbous herbs (Fig. 13, p. 19) with, generally, tubular hollow leaves and flowers in terminal umbels or heads enclosed, when young, in a membranous spathe of two or three leaves. Most of the forms have the characteristic odour of the onion. Among the pedicels small bulbs (**bulbils**) are commonly produced; these fall off and develop into new plants. This is a mode of vegetative reproduction. **Ramsons** (*A. ursinum*) is locally a common form—its leaves are thin and flat, not tubular. Cultivated forms of *Allium* include the **onion, garlic, shallot, leek**, &c.

Scilla includes small bulbous herbs with, generally, blue flowers in terminal racemes. The **bluebell** (*S. nutans*—sometimes *Hyacinthus nonscriptus*) is a very common spring flower in shady places. The **Siberian squill** (*S. sibirica*) and other forms are cultivated.

Colchicum is a small genus, including the **meadow saffron** (*C. autumnale*), an autumn-flowering bulbous herb. The ovary, although strictly superior, is borne underground, and at the bottom of a very long perianth tube which raises the upper part of the flower some inches above the surface of the ground. The foliage leaves do not reach their full development until the next spring, when the capsule is also raised to the surface of the ground.

Fritillaria includes the **snake's-head** or **common fritillary**, which is locally a common plant. The dull-red bell-shaped perianth is marked with chequered lines. The **crown imperial** (*F. imperialis*) and other fritillaries are cultivated.

Narthecium includes the **bog asphodel**, which is abundant on wet moors.

Tulipa includes the **wild tulip** (*T. sylvestris*), as well as the cultivated forms. The solitary terminal flower springs from a bulb ; the perianth leaves are free and the stamens hypogynous.

Lilium is not British, but many species are in common cultivation, including the **martagon lily** (*L. Martagon*), the **tiger lily** (*L. tigrinum*), the **white lily** (*L. candidum*), *L. auratum*, &c. Bulbils are produced in the axils of the upper leaves of *L. bulbiferum*.

Polygonatum (**Solomon's seal**) has a thick underground sympodial rhizome, drooping axillary flowers, and a leafy stem.

Convallaria (**lily of the valley**) has a creeping rhizome and radical leaves.

Ornithogalum includes the **star of Bethlehem** (*O. umbellatum*), with white and green flowers, but otherwise much like *Scilla*.

Muscari includes the **grape hyacinth** (*M. racemosum*), with globular dark-blue flowers, with six minute teeth. It occurs wild in a few localities and is also cultivated.

The **butcher's broom** (*Ruscus aculeatus*), the only British woody monocotyledon, produces numerous leaf-like flattened stems (**phylloclades**), which are formed in the axils of small scale leaves and bear unisexual flowers on their upper surfaces (Fig. 11, p. 18).

Asparagus also bears phylloclades, but in this case they are small and needle-like. The young shoots are edible.

Herb Paris (*Paris quadrifolia*) is a peculiar plant found locally. The flower is tetramerous, and is borne singly on the stem, which also bears a whorl of net-veined leaves. It is poisonous. Formula, P 4 + 4, A 4 + 4, $G\underline{(4)}$.

Among purely exotic forms we have the **aloe**, *Yucca*, and *Dracæna*, with thick fleshy leaves, **sarsaparilla** (*Smilax*) with net-veined leaves and stipular tendrils, **hyacinth** (*Hyacinthus*), &c.

The order is generally readily recognized by the six-leaved or six-lobed petaloid perianth, six stamens, and trilocular superior ovary with axile placentation. Floral formula (generally), P 3 + 3, A 3 + 3, $G\underline{(3)}$.

B. Ovary inferior.

** Order 8. **Orchidaceæ.** The orchid family (Fig. 177). This order, the largest among the monocotyledons, comprises nearly 350 genera and 5,000 species. They occur in nearly all countries, but are rare in cold climates, and most abundant in the damp forests of the tropics, where many are epiphytic on the stems and branches of trees.

Most of the European terrestrial forms have underground tubers or rhizomes. In the former case, two tubers occur together, the one soft and shrivelled, from which the flowering scape of the current year arises—the other firmer one has an apical bud, from which next year's shoot takes its origin. Some forms are rootless (e.g. *Corallorhiza*), while the tropical epiphytic forms have long aërial roots, covered with a special many-layered epidermis (the **velamen**), consisting of empty cells with reticulate thickenings capable of absorbing water-vapour and gases from the air (see Fig. 205, p. 432).

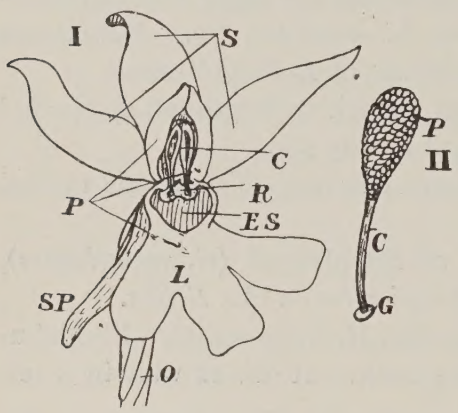


Fig. 177. Flower of *Orchis*. I. C=column; ES=entrance to the spur; L=labellum; O=ovary; P=the three inner perianth leaves; R=rostellum, below which is the stigma; S=the three outer perianth leaves; SP=spur. II. A pollinium (P) consisting of a mass of coherent pollen grains; C=caudicle; G=gland.

The leaves are entire and parallel-veined; sometimes foliage leaves are absent altogether and the plants are brown saprophytes, obtaining their organic matter from the soil, as in the British **bird's-nest orchis** (*Neottia Nidus-avis*). The flowers are very specially modified, and they are generally inverted by the twisting of the inferior ovary, so that the posterior side of the flower is apparently anterior and below.

The perianth has six petaloid segments in two whorls, of which the outer whorl is regular, or nearly so, while the posterior (lower) segment of the inner whorl is larger than the others, of a different shape, and frequently spurred (*Orchis*) or saccate (*Epipactris*)—it forms what is known as the **labellum**.

The stamens are theoretically six in number, but of these only one, sometimes two, are represented by fertile anthers (see floral diagram,

Fig. 159, I, p. 295); one or two others may be represented by staminodes. In the monandrous orchids (i. e. all except *Cypripedium*) it is the anterior stamen of the outer whorl which is fertile, while the two lateral staminodes belong to the inner whorl; in *Cypripedium*, the diandrous form, the fertile anthers belong to the inner whorl and represent the staminodes of *Orchis* and other monandrous genera, while the single staminode occupies the same position as the fertile anther of *Orchis*. The anther is two-lobed, and the pollen grains are usually completely united into masses (**pollinia**), one of which occupies each lobe of the anther; each pollinium is continued as a mucilaginous filament (the **caudicle**), which passes downward to the **rostellum**. The filament of the single stamen (or the filaments when there are two stamens) is adherent to the style, the two together forming the **column** or **gynostemium** in the centre of the flower.

The tricarpellary ovary is usually unilocular, with three parietal placentæ. In the monandrous forms the anterior lobe of the discoid stigma is not functional as a stigma, but often forms a special organ known as the rostellum, situated either below or above the anther. The caudicles of the pollinia adhere to small glands (**retinacula**) in the rostellum until they are removed by the agency of an insect. Below the rostellum, at the mouth of the spur, lies the viscid stigmatic surface.

The following are some of the British plants which belong to this order:—

The genus *Orchis* includes several common British species. The roots are tuberous, the leaves are often spotted, and the red or purple spurred flowers are arranged in terminal spikes. The **green-winged orchis** (*O. Morio*) has but few, six to eight, flowers in a loose spike. The **early spring orchis** (*O. mascula*) is common in shady and moist places, and the tuber is entire. The **spotted orchis** (*O. maculata*) also flowers in the spring, but its tubers are divided into finger-like processes. In both the last-named forms the leaves are usually spotted. The **marsh orchis** (*O. latifolia*) occurs in damp situations.

The genus *Habenaria* is closely related to *Orchis*. Perhaps the commonest form is the **butterfly orchis** (*H. bifolia*), which has spreading lateral outer perianth leaves, and a long narrow labellum. The flowers are white or slightly greenish in colour.

Aceras, including the **man orchis** (*A. anthropophora*), differs from *Orchis* in having spurless flowers. The man orchis is fancifully compared to a hanging man.

The genus *Ophrys* also has spurless flowers, but with a very convex labellum, which more or less resembles an insect's body. *O. apifera* is the **bee orchis**, and *O. muscifera* the **fly orchis**.

Epipactis includes the **marsh epipactis** (*E. palustris*) and the **broad epipactis** (*E. latifolia*). *Cephalanthera* is the **helleborine**.

The genus *Listera* includes the **common twayblade** (*L. ovata*), well marked by its pair of nearly opposite leaves a few inches above the ground, and also by the spreading perianth leaves.

Cypripedium, the **lady's-slipper**, is the diandrous form and is but rarely found in Britain. The labellum is yellow, and forms a shoe-like sac.

The order is recognized by the peculiar flowers. Floral formula (generally), P 3+3, A 1, $G\overline{(3)}$.

Order 9. **Amaryllidaceæ.** The amaryllis family. A large order, represented in Britain by three native genera only, *Narcissus*; *Galanthus*, the **snowdrop**; and *Leucojum*, the **snowflake**, but many others are cultivated and they constitute some of our most showy garden plants. The order is abundant in South Africa.

The plants are herbs, and possess a bulbous underground stem and a scape bearing either a single flower or a number of flowers enclosed, when young, in a membranous spathe.

The perianth is petaloid and in two whorls; it is generally regular, sometimes zygomorphic, and is often provided with ligular outgrowths, which form a **corona** springing from the tube of the perianth (Fig. 228, VIII, p. 485). The stamens are usually six in number, in two whorls, sometimes more numerous, either epiphyllous or epigynous. Gynæcium tricarpellary with a trilocular syncarpous inferior ovary, containing many ovules on axile placentæ. The fruit is generally a loculicidal capsule.

Narcissus has a gamophyllous perianth with a corona, and includes a number of cultivated forms, the **narcissi, daffodils, jonquils**, &c.

The **snowdrop** (*Galanthus*) and **snowflake** (*Leucojum*) have free perianth leaves without a corona. The former has a single flower on each scape, the latter a small number forming an umbel.

Forms in cultivation include *Amaryllis* with large handsome zygomorphic flowers; *Vallota*, also with zygomorphic flowers; *Crinum*; *Alstrœmeria*, the **Peruvian lily**, &c.

The genus *Agave* has rosettes of spiny succulent leaves borne on a short stem. The flowers are formed after vegetation has gone on for many years; a long scape arises which often bears thousands of

flowers, after which the plant dies from physiological exhaustion. These plants are often called **American aloes**, but the true **aloe** belongs to the *Liliaceæ*.

This order is readily recognized by the petaloid perianth, six stamens, and trilocular inferior ovary. Floral formula, P 3 + 3, A 3 + 3, $G\underline{(3)}$.

Order 10. **Iridaceæ.** The iris family. A large order which, like the *Amaryllidaceæ*, is abundantly represented in South Africa and other warm dry climates.

The plants are perennial herbs with bulbs (e.g. some species of *Iris*), corms (e.g. *Crocus*, *Gladiolus*, &c.), or rhizomes (e.g. most *Iris*). The linear leaves are in two rows (**distichous**); the margins of the older leaves overlap those of the younger ones, and are folded up the midrib (**equitant**). The flowers are generally regular, but sometimes zygomorphic, as in *Gladiolus*. The perianth is petaloid and in two whorls; stamens three, representing the outer whorl in the *Amaryllidaceæ*, anthers extrorse; gynæcium tricarpellary, forming a trilocular inferior ovary with axile placentæ (see floral diagram, Fig. 158, I, p. 294); styles often petaloid and spread over the stamens, with the stigmas on the under side, forming scale-like appendages. Fruit a loculicidal capsule.

The genus *Iris* includes two British species, the **yellow flag** (*I. Pseudacorus*), with yellow flowers, and the **fetid iris** or **roast-beef plant** (*I. fœtidissima*), as well as numerous cultivated exotic forms. The perianth segments are usually furnished with a row of hairs forming a 'beard,' on which a great part of the pollen falls. The flowers are provided with spathes.

The *Gladiolus* occurs wild only in a few localities in Britain; most of the species are South African. The flowers are zygomorphic and somewhat two-lipped.

The *Crocus* has radicle leaves arising from a corm; a one-flowered scape; regular flowers, each invested by a spathe; dilated and often fringed, but not petaloid, stigmas; and a subterranean ovary.

Other British genera are *Sisyrinchium* and *Romulea*. The cultivated forms include the **tiger flower** (*Tigridia*) with monadelphous stamens, *Ixia*, &c.

The order is recognized by the petaloid perianth, three stamens, and trilocular inferior ovary. Leaves often in two opposite rows. Floral formula, P 3 + 3, A 3 + 0, $G\underline{(3)}$.

CHAPTER XXII

THE DICOTYLEDONOUS ORDERS

I. Sub-Class Dichlamydeæ. Series A. Thalamifloræ.

** Order 1. **Ranunculaceæ.** The buttercup family (Fig. 178). The plants in this order, with the exception of *Clematis*, are herbs with alternate exstipulate leaves. There is complete absence of cohesion between members of the same whorl and of adhesion between those of different ones. The calyx consists generally of five sepals, and in the numerous genera in which the corolla is absent (e.g. *Anemone*, *Caltha*, *Clematis*), or in which the petals are modified into nectaries (e.g. *Aquilegia*, the **columbine**; *Delphinium*, the **larkspur**), the calyx is petaloid, and therefore attractive. The corolla consists typically of five petals; it may be regular (e.g. *Ranunculus*, the **buttercups**), or more or less irregular and zygomorphic (e.g. **larkspur, monkshood**). The stamens are generally numerous (indefinite) and hypogynous; the pistil is apocarpous with many carpels (e.g. *Ranunculus*) or few (e.g. **larkspur**).

The fruits in this order show as much variety as the flowers: in the **buttercups** and *Clematis* there is an etærio of typical achenes; in the **columbine**, the **monkshood**, the **marsh marigold**, &c., the fruit consists of a few follicles; in *Nigella* it is a capsule, and in the **baneberry** a single berry.

The following are the more important British genera of *Ranunculaceæ*:—

(i) *Ranunculus*, the **buttercups**. Regular flowers with indefinite stamens and carpels (Fig. 178, I, II, III). Each petal has a nectary near its point of insertion to the receptacle (Fig. 178, II). The **lesser celandine** (*R. Ficaria*) usually has only three sepals, and about eight or nine petals. The **water ranunculus** (*R. aquatilis*) has white flowers.

(ii) *Caltha*, the **marsh marigold**. Sepals large and yellow (petaloid); petals absent; carpels few (five to ten), developing into follicles.

(iii) *Clematis*. A climbing woody shrub with opposite pinnate compound leaves. Climbing by means of its petioles. Four greenish-

white sepals, corolla none. Fruit an etærio of achenes with persistent

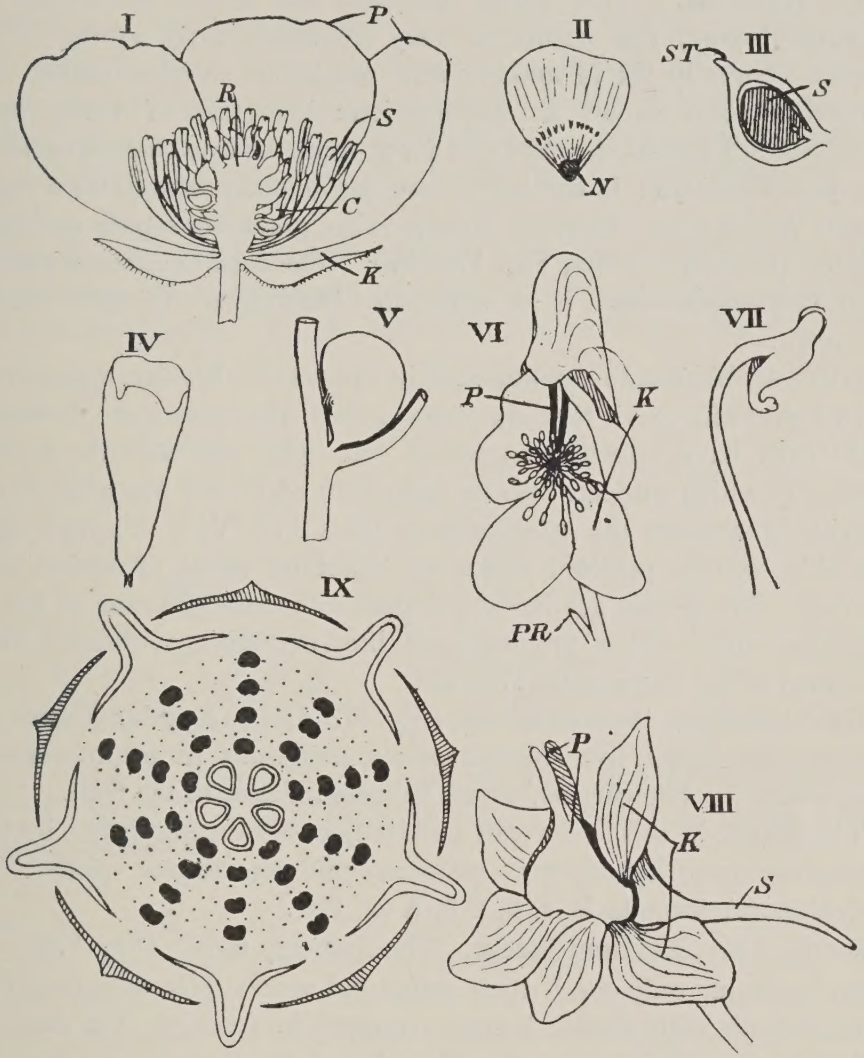


FIG. 178. *Ranunculaceæ.* I. Vertical section of flower of Buttercup (*Ranunculus*). C=carpels; K=sepals; P=petals; R=receptacle; S=stamens. II. A single petal of the Buttercup, showing the nectary (N). III. Section of a fruit (achene) of the Buttercup. S=albuminous seed; ST=stigma; the embryo is the small oval body at bottom of the seed. IV. A modified petal (nectary) of the Hellebore (*Helleborus*). V. Bulbil in the axil of a leaf of the Lesser Celandine (*Ranunculus Ficaria*). It becomes detached and forms a new plant. VI. Flower of Monkshood (*Aconitum*). K=calyx; P=modified petals; PR=one of the two bracteoles or prophylla. VII. One of the modified petals (nectaries) of the Monkshood. VIII. Flower of Larkspur (*Delphinium*). K=calyx; P=modified petals; S=spur of calyx. IX. Floral diagram of Columbine (*Aquilegia*). All the petals are spurred and the numerous stamens are arranged in whorls (cyclic).

styles which grow into long feathery awns and so assist in the dispersal of the fruits and seeds by the wind (Fig. 172, IV, p. 332).

(iv) *Thalictrum*, the **meadow rues.** Regular apetalous flowers with large anthers.

(v) *Anemone.* This genus includes the **wood anemone** and **pasque-flower,** the former a very common early spring flower. Sepals generally six in number and petaloid; corolla absent. The flowering stem shows a characteristic involucre of three leaves (bracteoles, Fig. 152, I, p. 284), either at some distance below, or near to the petaloid calyx: in the latter case the involucre simulates a calyx.

(vi) *Helleborus.* Regular flowers with greenish sepals and small tubular petals (nectaries, Fig. 178, IV). The fruit consists of follicles. The **Christmas-rose** is a hellebore indigenous to south-eastern Europe.

(vii) *Delphinium*, the **larkspur** (Fig. 178, VIII). Flowers zygomorphic with a petaloid calyx forming a spur: only two petals are developed, and these have appendages which join with one another to form a nectary which projects into the spur formed by the posterior sepal.

(viii) *Aconitum*, the **monkshood** (Fig. 178, VI). Flowers zygomorphic with a petaloid calyx, the posterior sepal of which forms a hood. The petals are inconspicuous, with the exception of the two posterior ones, which are modified into nectaries contained within the hood of the calyx (Fig. 178, VII).

(ix) *Aquilegia*, the **columbine** (Fig. 178, IX). Regular flowers with five petaloid sepals, five spurred petals, numerous whorls of stamens, and, generally, five carpels, which become follicles in the fruit.

The plants in this order are generally easily distinguished by their numerous, free, hypogynous stamens, and apocarpous pistil. The typical floral formula is K 5, C 5, A ∞, G $\underline{\infty}$.

* Order 2. **Berberidaceæ.** The barberry family (Fig. 179). An order including only one British genus and species (*Berberis vulgaris*). It is a shrub with simple leaves arranged in fascicles, i. e. shoots in which the internodes are undeveloped, and bearing elegant drooping racemes of yellow flowers. The leaves of the ordinary shoots are transformed into spines which bear the fascicled shoots in their axils.

Some cultivated forms have pinnate leaves (e. g. *Mahonia*). Calyx, corolla, and stamens in two whorls of three each; carpel solitary; fruit a berry.

The stamens are irritable and bend over towards the pistil if touched with a needle or by an insect (see p. 312); the anthers dehisce by valves (Fig. 179, III).

The order is distinguished by the trimerous calyx, corolla, and

androecium (dimerous in some exotics, e. g. *Epimedium*); the single carpel, and the valvular dehiscence of the anthers. The floral formula of *B. vulgaris* is K 3+3, C 3+3, A 3+3, $G\underline{1}$.

* Order 3. **Nymphæaceæ.** The water-lily family. Aquatic herbs with broad floating leaves, and rhizomes embedded in the mud at the bottom of the water. As is generally the case with water plants (see p. 97), the tissues (petioles, &c.) show many large air-containing spaces which serve to buoy the leaves, &c., to the surface of the water.

The flowers are large and solitary with four to five sepals, and numerous petals and stamens passing without any sharp demarcation into one another, an arrangement which is common when, as in this

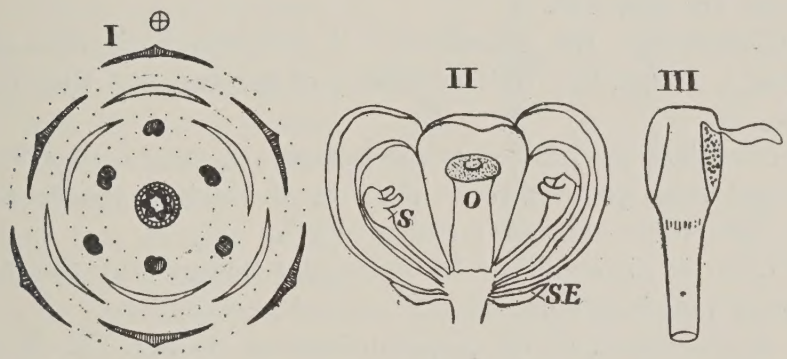


FIG. 179. *Berberidaceæ*. I. Floral diagram of the Barberry (*Berberis*), showing the trimerous arrangement of the perianth and stamens. II. Flower of the Barberry. O = ovary; S = stamens; SE = sepals. III. A single stamen of the Barberry, showing the mode of dehiscence by valves.

plant, the parts of the flower are arranged in a continuous spiral (acyclic) and not in whorls. Carpels numerous, forming a multilocular ovary with numerous seeds with both endosperm and perisperm (Fig. 170, VIII, p. 325). The British forms are the **white water-lily** (*Nymphæa alba*) and the **yellow water-lily** (*Nuphar luteum*, supra, p. 97). *Victoria regia* is a tropical American species which is remarkable for its large leaves.

The order is distinguished by its floating leaves and indefinite petals and stamens. The floral formula is generally K 4–5, C ∞, A ∞, $G(\underline{\infty})$.

* Order 4. **Papaveraceæ.** The poppy family. A very natural family of plants which includes about five British genera characterized by their regular flowers with dimerous calyx and corolla. The calyx

consists of two sepals which are valvate in the bud and fall off as the flower opens (caducous); the corolla of four free petals in two whorls; numerous stamens in alternating whorls; and a syncarpous ovary of two or more carpels containing numerous ovules.

The following are the best known British genera:—

(i) *Papaver*, the **poppies**. Herbs with milky latex contained in **laticiferous vessels**, which are formed as in the *Compositæ* (see p. 450). Carpels numerous, forming a unilocular ovary with many radiating partitions, which pass towards but do not meet at the centre. The fruit is a porous capsule, capped by the sessile radiate stigma, and containing a large number of seeds scattered over the surface of the radiating septa (Fig. 168, I, II, p. 321). *P. somniferum* is cultivated in the East, and its latex yields the opium from which morphia and laudanum are prepared.

(ii) *Chelidonium*, the **celandine**. A common herb with orange latex and a siliqua-like fruit consisting of two carpels. Placentation parietal.

(iii) *Glaucium*, the **horned** or **sea poppy**. A stout herb with thick leaves and large yellow flowers, the fruit of which, consisting of two carpels, sometimes becomes a foot in length.

The order is distinguished by its regular flowers with two sepals, four petals, indefinite stamens, and parietal placentation.

The floral formula of the **poppy** (*Papaver*) is K 2, C 2+2, A ∞, G $\underline{(\infty)}$; of *Chelidonium*, K 2, C 2+2, A ∞, G $\underline{(2)}$.

** Order 5. **Cruciferæ.** The wallflower family (Fig. 180). A very large and natural extra-tropical order represented in Britain by some twenty-seven genera including many very useful cultivated forms, e. g. **cabbage**, **cauliflower**, **turnip**, **mustard**, **watercress**, **radish**, &c., and others which are grown for the sake of their flowers, e. g. **wallflower**, **stock**, **candytuft**, &c. There are no poisonous plants in the order.

The leaves are alternate and exstipulate (i. e. without stipules); the flowers are arranged in leafless (ebracteate) racemes commonly more or less corymbose.

The parts of the flower are entirely free, with the exception of the pistil, which is syncarpous; the flower as a whole being, generally, regular and isobilateral, as it is divisible into symmetrical halves in two planes, antero-posterior and lateral (see floral diagram, Fig. 157, IV, p. 293).

The calyx consists of four sepals in two whorls; the corolla of four

petals in one whorl; the androecium of six stamens, the two outer lateral ones being shorter than the four inner ones (tetradynamous); and the pistil of two lateral carpels containing ovules or parietal placentæ. From the placentæ a false partition arises which grows inward and makes the ovary and subsequently the fruit bilocular. The fruit is very characteristic of the order: when ripe the two carpels split away from the false septum and placentæ, which now form a kind of frame called the **replum**, to which the seeds are attached (Fig. 180, IV, **V**, VI). The false septum with its replum remains attached to the apex of the pedicel and the seeds afterwards drop off. Such a fruit as that of the wallflower, which is much longer than broad, is described as a **siliqua**, while the short broad forms such as are seen in **honesty** (Fig. 180, VI) and **shepherd's purse** (*Capsella*) are called **siliculas**. Some few genera have fruits of a different type: these may be indehiscent and one-seeded as in **woad** (*Isatis*), or indehiscent but breaking into one-seeded portions as in the **radish**, &c.

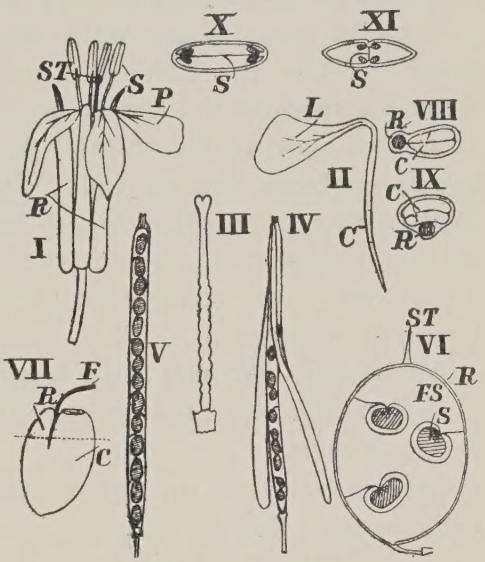


FIG. 180. *Cruciferæ*. I. Flower of *Brassica*. P=petals; R=the two inner sepals; S=tetradynamous stamens; ST=stigma. II. A single petal of *Brassica*, showing the narrow claw C and expanded horizontal limb L. III. Fruit of *Brassica*. A siliqua somewhat constricted between the seeds. IV. Dehiscing fruit of the Wallflower (*Cheiranthus*). The two valves are seen separating from below upwards, leaving the seeds attached by their long stalks (funicles) to the marginal placenta (replum). V. The same after complete removal of valves. VI. Fruit of Honesty (*Lunaria*). A silicula (short and broad). FS=false septum; R=replum; S=flattened winged seeds attached to the replum; ST=style. VII. Seed of Wallflower. C=cotyledons; F=funicle; R=radicle. VIII. Section of accumbent seed. C=cotyledons; R=radicle. IX. Section of incumbent seed. C=cotyledons; R=radicle. X. Section of latisept fruit. S=septum. XI. Section of angustisept fruit. S=septum.

The order is commonly divided into four sub-orders according to the characteristics of the fruit:—

(i) **Siliquosæ**. Fruit a siliqua, much longer than broad. The following are some of the more important genera and species included in this division:—

Cheiranthus, the **wallflower**. At the base of the two shorter stamens are the green nectaries, lodged in a sac at the base of the

two inner sepals. In the ripe seed, which is formed from a campylotropous ovule, there is a long funicle, an absence of endosperm (one layer of endosperm cells is said to be persistent), and the cotyledons are bent back parallel to the radicle so that their edges are turned towards it (**accumbent**, Fig. 180, VII, VIII).

Matthiola, the **stocks** of our gardens.

Brassica includes the **wild cabbage** (*B. oleracea*) and its cultivated varieties, the **kohl-rabi** with the stem swollen at the base, **Brussels sprouts**, the leaf-buds of which are eaten, **cauliflower** with masses of abortive flowers and fleshy coherent peduncles, **broccoli, savoy cabbage, Scotch kale**, &c. The **turnip** (*B. rapa*), **wild rape, Swedish turnip, white** and **black mustard**, &c., belong to this genus, and also the **wild mustard** or **charlock** (*B. sinapis*) one of the commonest of weeds. All the species of *Brassica* have yellow flowers.

Nasturtium officinale is the **watercress.**

Alliaria officinale, the **hedge-mustard**, is one of the commonest of spring flowers.

Cardamine pratensis, the **cuckoo-flower**, is a pretty spring and early summer flower.

(ii) **Siliculosæ.** Fruit a silicula, short and broad. In this division are included the following (among other) plants:—

Lunaria biennis or **honesty.** The fruit (Fig. 180, VI) is nearly round, and the large flattened winged seeds show their mode of attachment to the parietal placentæ very clearly. The fruit is flattened parallel to the septum (**latisept**, Fig. 180, X): this character is used in classification (see *Capsella* below).

Cochlearia armoracia is the **horse-radish**, the thick roots of which are eaten.

Capsella Bursa-pastoris, the **shepherd's purse**, is found everywhere as a weed. The somewhat triangular fruits are flattened at right angles to the septum (**angustisept**, Fig. 180, XI). The seeds are incumbent, as the radicle lies on the back of one of the cotyledons (Fig. 180, IX). See *Cheiranthus* above.

Iberis (**candytuft**). Corolla zygomorphic.

Lepidium, the **cresses.** Fruit angustiseptal with one seed only in each cell.

(iii) **Nucumentaceæ.** Fruit indehiscent and few-seeded. This division includes *Isatis tinctoria*, the **dyer's-woad**, the leaves of which yield a blue dye which is supposed to have been used by the ancient Britons. The flat pods contain single seeds only.

(iv) **Lomentaceæ.** Fruit constricted into one-seeded portions (**lomentaceous**), indehiscent but breaking transversely between the seeds.

Raphanus is the **radish.** The pod is generally many-seeded, and has no longitudinal partition when ripe; it ends in a long style.

Cakile (**sea-rocket**) and *Crambe* (**sea-kale**) are common maritime plants belonging to this division; the fruit is two-jointed, but only the upper one may develop a seed.

The plants in this order are easily recognized by the four sepals and petals, the tetradynamous stamens, and characteristic ovary and fruit. The floral formula is K 2+2, C×4, A 2+2^2, G$\underline{(2)}$. [The sign × after the C indicates that the petals are diagonal, 2^2 that the inner whorl of four stamens probably represents two branched ones.] See floral diagram, Fig. 157, IV, p. 293.

Order 6. **Violaceæ.** The violet family (Fig. 166, p. 313). An order consisting of the British genus *Viola* with irregular (zygomorphic) flowers, and some exotic plants (African and South American) with regular ones.

The leaves are stipulate, and either radicle or alternate: the flowers are borne singly in the axils of the leaves (Fig. 151, V, p. 282).

The sepals are produced at the base beyond their points of insertion into outgrowths called **auricles**; the anterior (lower) petal is produced into a long spur sheathing two long nectaries which grow out from the connectives of the two antero-lateral stamens; the stamens have prolongations of their connectives beyond the anthers (Fig. 166, II, p. 313); the ovary is unilocular and consists of three carpels with parietal placentæ (Fig. 156, I, p. 292); the fruit is a capsule which splits loculicidally into three valves, each valve bearing a row of seeds. Most of the plants in this order produce two kinds of flowers, the showy perfect ones which, although wonderfully adapted for insect pollination (see p. 312), produce but little seed, and inconspicuous, nearly apetalous, closed (cleistogamous) flowers, which appear later on in the season, are self-fertilized, and form capsules full of seed (see p. 312).

The genus *Viola* includes:—

The **sweet violet** (*V. odorata*), which has an underground stem with runners, and leaves with narrow stipules. There are two bracteoles (as in the pansy, Fig. 151, p. 282) and a pointed stigma (Fig. 156, p. 292). The cleistogamous flowers are found in summer among the lower leaves; they look like small vegetative buds.

The **dog-violet** (*V. canina*) is much like the sweet violet, but has pale scentless flowers.

The **heartsease** (*V. tricolor*) and its variety the **pansy** (Fig. 151, V, p. 282, and Fig. 156, I, p. 292). We may notice the large leafy stipules and the two bracteoles or prophylls on the flower stalk : also the coloured lines on the petals (guiding lines for insects), all directed towards the centre of the flower and the nectary. Owing to the cohesion of the anthers a space is enclosed between their prolongations and the style, and this space contains the shed pollen. The stigma is nearly globular, and has a projecting lip and a deep cavity which is the only part of the stigma capable of receiving pollen. For the mode of pollination see p. 312. This is the only species of *Viola* in which the large showy flowers generally form seed, and in which cleistogamous flowers are not formed.

The order is recognized by the spurred flowers, the extension of the connectives of the stamens above the anthers, and the three parietal placentæ in the ovary. Floral formula, K 5, C 5, A 5, $G\underline{(3)}$.

** Order 7. **Caryophyllaceæ.** The pink family (Fig. 181). A large order consisting of herbs with opposite, decussate, sessile, entire leaves, springing from nodes usually more or less swollen.

The inflorescence is commonly a typical dichasial cyme passing in its ultimate branches into a monochasial form (Fig. 181, I, and Fig. 164, I, p. 303). The flowers are regular and actinomorphic; the calyx consists of five, sometimes only four, sepals, either free or coherent; petals equal in number to the sepals and often deeply divided so as to appear double in number (Fig. 181, IV), sometimes absent or very small (e.g. **procumbent pearlwort**, *Sagina procumbens*); stamens generally double in number to the sepals or petals and in two whorls, the inner whorl sometimes absent (e.g. *Sagina procumbens*, &c.); gynæcium of two, three, or five carpels with many ovules on a free central placenta formed by the breaking down of the original dissepiments (Fig. 181, III), traces of which can often be seen; styles free and indicating the number of carpels; fruit and capsule dehiscing by teeth at the top (Fig. 181, V).

The order is divided into the following sub-orders :—

(i) **Sileneæ.** Calyx gamosepalous.

This division includes the following genera :—

Dianthus, the **pinks** and **carnations.** The calyx is surrounded at its base by a number of decussating bracteoles. Two carpels and styles.

Silene, the **catchfly**. *S. inflata* is the **bladder campion**. *S. maritima* is a sea-coast form with thick leaves. *S. nutans* is the **Nottingham catchfly**. *Silene* has three carpels.

Lychnis, the **campion**, has five carpels and styles. The **white** and **red lychnis** (*L. vespertina* and *diurna*) are common and usually dicœcious herbs. The **ragged robin** (*L. Flos-cuculi*) (Fig. 181, I) has its petals cut into linear lobes. There is an outgrowth at the

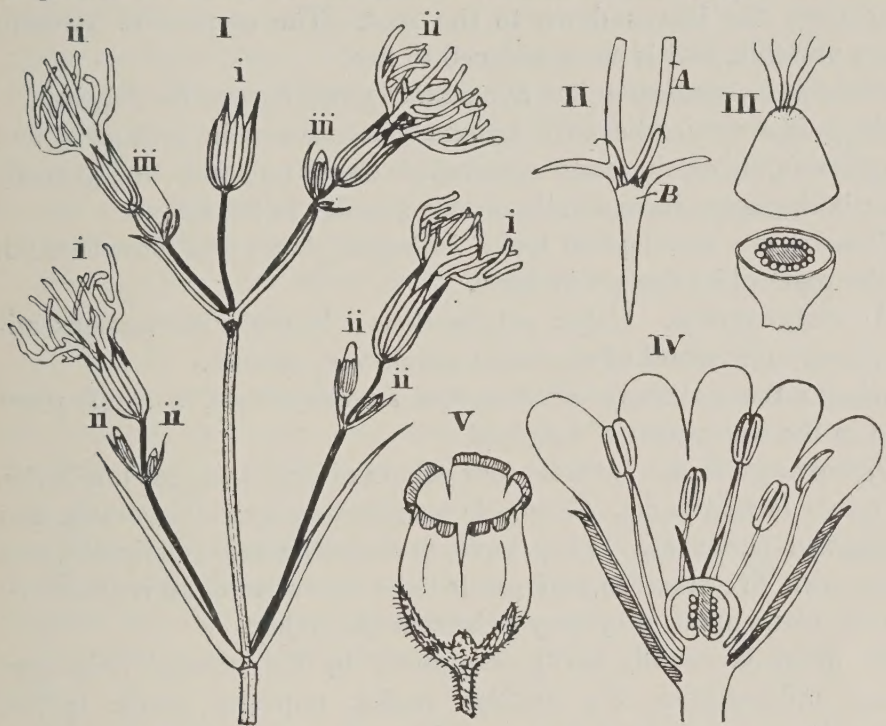


FIG. 181. *Caryophyllaceæ*. I. Ragged Robin (*Lychnis Flos-cuculi*), showing the dichasial inflorescence. Three dichasial cymes are represented; in each system the flower i opens first, the flowers ii, ii next, and so on. II. A single petal of the same, showing the limb A and claw B, the former deeply divided. Notice the outgrowth at the junction of claw and limb. III. Ovary of same, showing the free styles and free central placentation. IV. Vertical section of flower of *Stellaria*, showing the deeply bifid petals, two whorls of stamens, &c. V. Ripe capsule of *Lychnis*, showing dehiscence by teeth.

junction of the claw and limb of the petals (Fig. 181, II). This is also seen in the other species. The **corn-cockle** (*L. Githago*) is common in cornfields.

Saponaria, the **soapwort**, resembles *Lychnis*, but has only two styles.

(ii) **Alsineæ**. Calyx polysepalous.

This division contains the following genera:—

Cerastium includes the **common mouse-ear chickweed** (*C. vul-*

gatum, or *C. triviale*). The two whorls of stamens should be noted and the order in which they mature and shed their pollen. The flower is protandrous (see p. 310). The capsule is cylindrical and curved.

Stellaria includes the **common chickweed** (*S. media*), the **lesser stitchwort** (*S. graminea*), the **greater stitchwort** (*S. Holostea*), &c. There is a line of hairs down the stem of *S. media* which conducts water from the leaves down to the root. The number of stamens is very variable, and is often reduced to five.

Holosteum umbellatum has five stamens and flowers in umbels.

Spergula arvenis, the **corn spurrey**, is common in cornfields, and *Spergularia rubra*, the **sand spurrey**, is found on sandy and gravelly soils ; both genera have small scarious stipules to the leaves.

Mœnchia is a small plant found in waste places and elsewhere ; it has the parts of its flowers in fours.

(iii) **Polycarpeæ.** Calyx polysepalous ; leaves with scarious stipules ; only one whorl of stamens ; petals very minute.

Includes the **polycarp** (*Polycarpon tetraphyllum*), a small plant found in the south-west of England.

(iv) **Paronychieæ.** Includes four genera of inconspicuous low herbs, *Corrigiola* (**strapwort**), *Herniaria* (**rupture-wort**), *Illecebrum*, and *Scleranthus* (**knawel**). They have, generally, scarious stipules, and flowers with five stamens and petals ; the latter are often represented by small filaments or they may be absent altogether.

The order is usually easily recognized by the general habit and cymose inflorescence, the swollen nodes, opposite entire leaves, regular flowers, definite stamens, and free central placentation. The floral formula is generally K (5), C 5, A 5+5, $G\underline{(2-5)}$. See floral diagram, Fig. 157, III, p. 293.

* Order 8. **Hypericaceæ.** The St. John's wort family. Represented in Britain by one genus only (*Hypericum*) with about a dozen species.

The plants are generally perennials with opposite, entire, exstipulate leaves, commonly marked with translucent oil-glands, easily seen when a leaf is looked through. The flowers (Fig. 154, II, p. 290) are regular and the stamens indefinite ; the latter are arranged into three or five bundles (polyadelphous). Styles free. Axile placentation.

The order is readily recognized by the opposite leaves, pellucid glands, regular flowers, and, especially, by the polyadelphous stamens. Floral formula, K 5, C 5, A 3–5 × ∞, $G\underline{(3—5)}$. [The

symbol A 3–5 × ∞ indicates that there are 3–5 stamens indefinitely branched.]

Order 9. **Malvaceæ.** The mallow family. The leaves in this order are generally simple, alternate, stipulate, and palmately veined: flowers regular, and for the British genera very characteristic. The calyx is valvate in the bud and the petals are twisted (contorted); the stamens are numerous and really represent five branched stamens opposite the petals (antipetalous); the filaments are united into a tube (monadelphous, Fig. 154, I, p. 290), or, in *Tilia*, into five antipetalous bundles (polyadelphous); carpels generally numerous and cohering into a characteristic multilocular ovary with one ovule in each loculus (except *Tilia*, which has a pentalocular ovary with two ovules in each loculus); fruit generally a schizocarp splitting into one-seeded portions or cocci (Fig. 167, III, p. 319).

The following are some of the principal genera and species belonging to this family:—

Malva, the **mallow.** This genus includes three native species, as well as the **tree mallow** (*M. mauritiana*), the **curled mallow** (*M. crispa*), and other cultivated forms. All the species have an involucre (epicalyx) of three free bracteoles just under the flower, and, indeed, inserted on the calyx (Fig. 152, III, p. 284).

Althæa includes the **marsh mallow** (*A. officinalis*) with an epicalyx of six to nine leaves which are joined together at the base. The **hollyhock** (*A. rosea*) is a Mediterranean species.

Lavatera is the only other British genus. Its involucre is three-lobed.

Tilia, the **lime-tree.** The inflorescence is generally a few-flowered cyme, the peduncle of which is adnate for a part of its length to a large leafy bract. The peduncle, bract, and a small resting bud, which grows into a leafy branch in the following season, all appear to be situated in the axil of a single leaf; the explanation of which is as follows:—The large adnate bract and one of the bud-scales of the resting bud are really the first two leaves of the axillary branch which terminates in the inflorescence; the winter bud arises in the axil of the before-mentioned bud-scale. The flowers have deciduous sepals and numerous stamens, often more or less united into five bundles (polyadelphous) which lie opposite to the petals. The ovary is five-celled, with two ovules in each loculus; the style simple, but branched above; fruit generally one-seeded only, as all the ovules except one are aborted.

Exotic cultivated forms include *Abutilon*, which has no involucre, *Hibiscus*, with many-seeded carpels forming a capsular fruit, and *Gossypium*, the **cotton-plant**, which also has a capsular fruit. Cotton consists of the delicate long hairs which cover the seeds of many species of this genus.

The British genera belonging to this order (except *Tilia*, which is often placed in an order by itself) may be recognized by the regular flowers with valvate sepals, twisted (contorted) petals, monadelphous stamens, and characteristic ovary and fruit.

Floral formula of *Mallow*, &c. K (5), C 5, A $(5 \times \infty)$, G $\underline{(\infty)}$.

„ „ *Tilia* K 5, C 5, A $5 \times \infty$, G $\underline{(5)}$.

[The symbol A $5 \times \infty$ indicates that the five stamens are indefinitely branched.]

Order 10. **Geraniaceæ.** The geranium family (Fig. 182). This familiar order consists of plants, most of which have simple, palmately or pinnately veined, or sometimes peltate, leaves. Some, e. g. *Oxalis*, have compound leaves. Leaves stipulate or exstipulate. The flowers are generally regularly pentamerous, with two whorls of stamens, and **obdiplostemonous**, i. e. with the outer stamens opposite to the petals, and the inner opposite to the sepals—a reversal of the normal alternation of petals and stamens (see floral diagram, Fig. 157, II, p. 293); sometimes the flowers are spurred and therefore zygomorphic; the filaments of the stamens are united at the base (monadelphous) and hypogynous; the carpels are often prolonged upwards into a long beak or **carpophore** (Fig. 182, III, IV) which, after flowering, may grow to a length of some inches; the stigmas are free; each of the five carpels contains two suspended ovules, but only one matures; placentation axile.

The fruit is characteristic. In *Geranium*, *Pelargonium*, and *Erodium* it is a schizocarp, separating septicidally into five one-seeded **cocci**, which roll up from below, while they are attached to long elastic **awns** (the styles) which were connate with the central column. When the fruit is mature the liberation of the cocci may take place suddenly, so that the latter are scattered to some distance; in the **stork's-bill** (*Erodium*) and in *Pelargonium* the partial fruits (cocci) are forced into the ground by the movements of their hygroscopic awns. In some other cases the seeds are forcibly ejected, while their carpels remain attached to the central column by the upper ends of the awns.

The genus *Geranium* includes about a dozen British wild species,

one of the commonest of which is the herb Robert (*G. Robertianum*). There is a gland at the base of each of the inner (antisepalous) whorl of stamens. In the dehiscence of the fruit the seeds remain enclosed in the carpels.

Pelargonium. This Cape genus includes many of the species in cultivation—the 'garden geraniums.' The posterior sepal is larger than the others, and is provided with a long spur which is adherent to the pedicel, and may be seen by cutting the latter across; the flower is in consequence zygomorphic (Fig. 182, I, II).

Erodium, the stork's-bill, differs from *Geranium* in several respects;

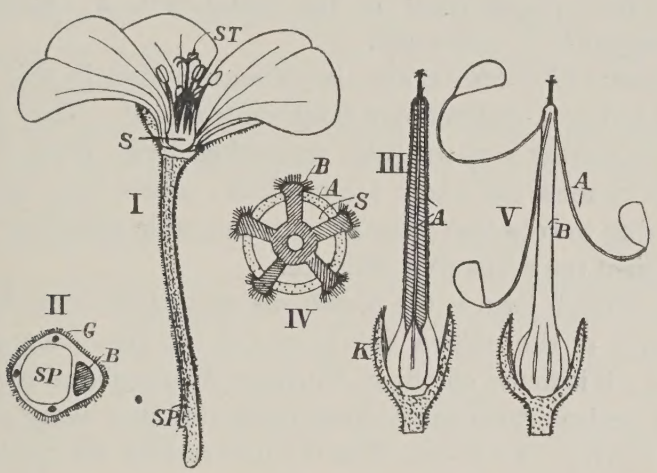


FIG. 182. *Geraniaceæ.* I. Flower of *Pelargonium.* The sepals and petals of one side have been removed. S=monadelphous stamens; SP=end of adherent spur; ST=the five free stigmas. II. Transverse section across pedicel and spur. B=vascular tissue of pedicel; G=glandular hairs; SP=cavity of spur. III. Fruit of *Pelargonium.* A=the adherent styles which become detached from the central column (carpophore) and form the awns; K=persistent calyx (the sepals in front have been removed). IV. Transverse section across carpophore. A=the separating parts of the axis; B=the wheel-shaped persistent part of the axis; S=space. A become the awns. V. Ripe fruit of *Pelargonium*, showing the cocci separating from the axis B. A=the awns.

the leaves are pinnately, not palmately, veined and lobed; the stamens are only five in number, as the antipetalous ones are represented by staminodes only; and the awns of the carpels are spirally twisted after their detachment from the central axis.

Oxalis Acetosella, the wood-sorrel, is a common plant found in woods, and differs from *Geranium* in several respects, and so is often placed in a distinct order (Oxalidaceæ). The leaves are compound, with three leaflets (ternate), like those of a clover; there is no beak to the flower or fruit, and the fruit is a capsule with several seeds. This plant, like the violet, has cleistogamous flowers. The leaves

show sleep-movements—at night, or if irritated, or even in cloudy weather, the leaflets lie in a vertical plane, resuming their horizontal position again during the day. During the night the leaves are protected in this way from excessive radiation of heat and consequent injury by cold (see p. 467).

The South American *Tropæolums* may be included in this order, but are often made into a distinct one (**Tropæolaceæ**). They have peltate exstipulate leaves, spurred flowers, and eight stamens. The fruit consists of three one-seeded carpels, which separate from the axis when ripe. *T. majus* is the **Indian cress** or **garden nasturtium** (the true *Nasturtium* is the watercress, a crucifer). The **canary creeper** is *T. aduncum.*

The **balsams** (*Impatiens*) are also often included in this order, but may be made into a distinct one (**Balsaminaceæ**). They differ from *Geranium* in having very irregular spurred flowers. Only three sepals can usually be seen, and these are petaloid; petals five, but appearing as three owing to cohesion; the fruit is a capsule dehiscing elastically so as to project the seeds to a distance.

The only British form is the **touch-me-not** (*I. Noli-me-tangere*), so called because of the sudden dehiscence of the ripe fruits when they are touched; it is found chiefly in Northern England and North Wales. A North American form has become fairly common along some of the streams in Surrey, and several East Indian species are cultivated.

The plants in this order in its restricted sense, i. e. including *Geranium*, *Pelargonium*, and *Erodium*, are usually recognized by the regular (or nearly regular) pentamerous flowers, the definite stamens which are often monadelphous, the beak-like carpophore, free styles, and characteristic fruit.

Floral formula of *Geranium* and *Oxalis*, K 5, C 5, A (5+5), G$\underline{(5)}$.

" " *Erodium* K 5, C 5, A † 5+5, G$\underline{(5)}$.

" " Balsam K 5, C 5, A 0+5, G$\underline{(5)}$.

[The symbol A † 5+5 indicates that the outer whorl of stamens is represented by staminodes; A 0+5 that the outer whorl is absent altogether. For floral diagram of *Geranium*, see Fig. 157, II, p. 293.]

* Order 11. **Aceraceæ.** The maple family. Trees with opposite, palmately veined and lobed exstipulate leaves (Fig. 225, I, p. 481), and regular greenish flowers, arranged in racemes. The number of members in each whorl of the flower is somewhat variable, but as a rule there are five sepals, five petals, eight stamens, and two carpels. The ovary is bilocular, with two ovules in each loculus, and develops into

the characteristic fruit, a double samara (schizocarp) which splits when ripe into two one-seeded winged mericarps, which are at first attached to a branched carpophore (Fig. 167, II, p. 319). A large disc is present.

The **common maple** (*Acer campestre*) has short erect racemes of flowers, and a fruit the wings of which spread horizontally so as to form one straight line.

The **sycamore** (*Acer Pseudoplatanus*) has pendulous racemes and a fruit with nearly parallel wings. This is generally a larger tree than the maple.

Many exotic species of *Acer* are cultivated, especially North American forms, some of which have only five stamens, and diœcious flowers. Sugar is prepared from the sap of some North American species (*A. saccharinum*, &c.).

The order is recognized by the opposite palmately lobed leaves, definite stamens, and characteristic fruit. Floral formula generally, K 5, C 5, A 8, G(2).

[The **horse-chestnut** (*Æsculus Hippocastanum*) belongs to the **Sapindaceæ**, a closely related order, of which the **Aceraceæ** is often made only a tribe. The leaves are palmately compound, and consist of seven leaflets; the inflorescence is a branched cymose raceme, with hermaphrodite and staminal flowers (polygamous), of which only the lower ones produce fruit; the fruit is a fleshy capsule divided into three chambers.]

Series B. Calycifloræ.

** Order 12. **Rosaceæ.** The rose family (Figs. 183, 184). This large and important family consists of trees, shrubs, and herbs, and is widely spread over the globe, more especially in the cooler parts of the northern hemisphere. The British forms, belonging to some sixteen genera, show great variation in the structure of their flowers, especially of their gynæcia and fruits.

Leaves alternate, simple or compound, and stipulate; flowers regular, actinomorphic; odd sepal posterior (not anterior, as in **Leguminoseæ**); stamens generally indefinite and perigynous; number of carpels various, from one to an indefinite number, and apocarpous, or spuriously syncarpous; ovary generally superior; fruit various.

The order is conveniently divided into a number of sub-orders, or tribes, as follows:—

(i) **Roseæ.** The rose tribe (Fig. 183, I, II, III, IV). Carpels numerous in a deeply concave cup-shaped receptacle, to the margin of which

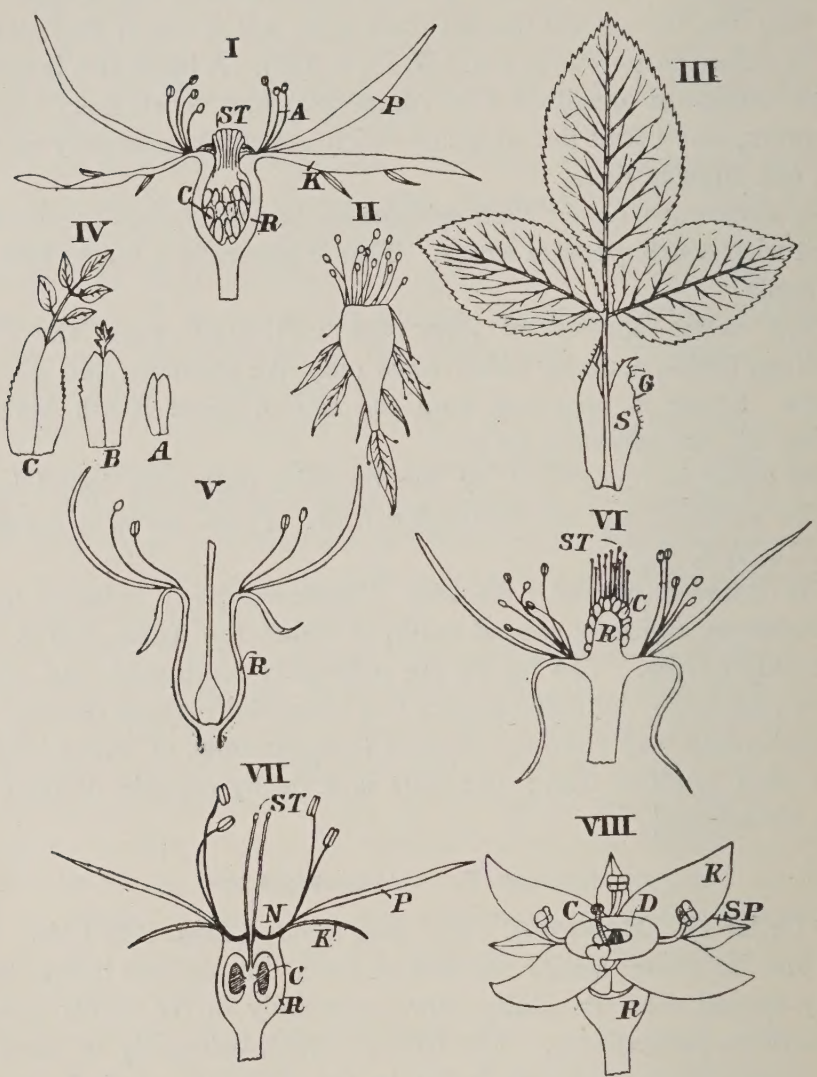


FIG. 183. *Rosaceæ*. I. Vertical section of flower of the Dog-rose. A = perigynous stamens; K=sepals; P=petals; R=hollow receptacle, on the inner side of which the free carpels (C) are inserted; ST=free styles. II. One of the sepals from I with its attached stamens. III. Compound leaf of *Rosa* with its adnate stipules (S). G=glandular hairs. Most of the leaves of the rose have more leaflets than the one shown here. IV. Bud-scales of the Rose. A is one of the outermost scales, and consists of nothing but the leaf-base (compare III). B and C are inner scales; they exhibit small laminæ. V. Vertical section of the flower of the Cherry, showing a single carpel seated at the base of the receptacular cup (R). VI. Flower of the Dewberry, showing the convex receptacle (R) on which are seated numerous free carpels (C). ST=stigmas. Notice the perigynous insertion of the petals and stamens. VII. Vertical section of the flower of the Apple. C=the carpels and ovules contained in and adnate to the receptacular cup (R); K=sepals; N=nectary; P=petals; ST=stigmas. VIII. Flower of *Alchemilla*. C=the single carpel and style; D=glandular yellow disc (nectary); K=sepals; R=receptacular cup; SP=epicalyx.

the petals and numerous stamens are attached; carpels one-seeded, becoming achenes in the fruiting stage, enclosed in the fleshy receptacle; sepals persistent. Leaves compound (pinnate), with adnate stipules, e. g. the **field-rose** (*Rosa arvensis*), **dog-rose** (*R. canina*), **sweetbriar** (*R. rubiginosa*), &c.

(ii) **Spiræeæ.** The meadow-sweet tribe. Carpels generally five in number, inserted on a flat receptacle; fruit an etærio of follicles; calyx persistent.

The **meadow-sweet** (*Spiræa Ulmaria*) has pale cymose flowers and pinnate leaves in which pairs of larger leaflets alternate with smaller ones. *S. Filipendula* is the **dropwort.**

(iii) **Pruneæ** (Fig. 183, V). One carpel only, attached to the bottom of a cup-shaped receptacle; the receptacle does not persist to the fruiting stage; only one of the two ovules develops into a seed; fruit a drupe (Fig. 184, IV). Trees with simple leaves. The **blackthorn** or **sloe** (*Prunus spinosa*) has spinous branches, and flowers which appear before the leaves. This form is believed to be the ancestor of all our cultivated **plums** and **damsons.** **Wild cherry** (*P. Cerasus*); **bird-cherry** (*P. Padus*); **apricot** (*P. Armeniaca*); **peach** (*P. Persica*), &c.

The **almond** (*P. Amygdalus*) forms a fibrous, not a fleshy, drupe (Fig. 184, V). *Prunus Laurocerasus* is the **cherry laurel.**

(iv) **Potentilleæ.** Characterized by the presence of a convex receptacle on which numerous free carpels are inserted. Stamens indefinite (Fig. 183, VI). An epicalyx is generally present, formed of the connate stipules of the calyx leaves.

The genus *Potentilla* has flowers which often resemble the buttercups, but differs from them in the perigynous, not hypogynous, insertion of the petals and stamens. Fruit an etærio of achenes on a dry receptacle.

The **strawberry** (*Fragaria*) differs from *Potentilla* only in the fruit, which consists of an etærio of achenes scattered over the surface of a fleshy receptacle (Fig. 184, I).

In the genus *Rubus*, including the **blackberry, dewberry, raspberry,** &c., there is no epicalyx, and the fruit is an etærio of drupels on a nearly dry conical receptacle (Fig. 184, II, III).

Geum has an epicalyx, leaves with large leafy stipules, and a dry fruit consisting of an etærio of achenes, each of which ends in a long awn, which is hooked at the tip to assist in dispersal by animals (Fig. 184, VII).

Dryas octopetala, the **mountain avens**, is a northern form, with eight sepals and petals.

(v) **Pomeæ**. The apple and pear tribe (Fig. 183, VII). In this

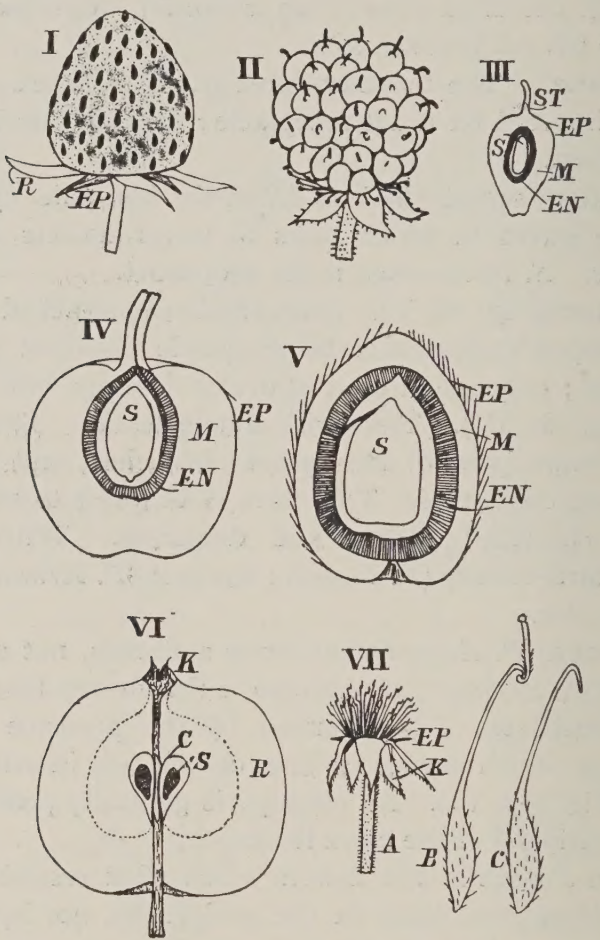


FIG. 184. Rosaceous fruits. I. Strawberry. An etærio of achenes on a succulent receptacle. EP=epicalyx; R=persistent calyx. II. Blackberry. An etærio of drupels. Persistent calyx and stamens. III. Section of a single drupel of the same. EN=endocarp; EP=epicarp; M=mesocarp; S=seed; ST=style. IV. Section of the fruit of the cherry. A simple drupe. EN=endocarp; EP=epicarp; M=mesocarp; S=seed. V. Section of the fruit of the Almond. A fibrous drupe. EN=endocarp; EP=epicarp; M=mesocarp; S=seed. VI. Section of the fruit of the Apple. C=wall of carpel; K=remains of calyx; R=succulent receptacle; S=seed. VII. Fruit of Avens (*Geum*). (A) Complete fruit (an etærio of achenes) with persistent calyx (K) and epicalyx (EP). (B) One of the achenes from a nearly ripe fruit. Note the peculiar curve in the style just below the stigma. (C) Older fruitlet from which the terminal portion of the style and the stigma have broken off, leaving the characteristic sharp hook.

division the carpels are contained in, and are adnate to, a cup-shaped receptacle, which is closed at the top, so that the ovary and fruit are inferior and spuriously syncarpous. The fruit, a pome, is generally

surmounted by the remains of the calyx (Fig. 184, VI). The plants are shrubs or trees.

The **apple** (*Pyrus Malus*) and **pear** (*P. communis*) have five carpels, with thin coriaceous walls, forming the core of the fruit, and each containing seeds: the whole is surrounded by the thick fleshy receptacle (Fig. 184, VI). The cultivated apples and pears are all varieties of these two wild species.

The **white beam-tree** (*P. Aria*) and **wild service-tree** (*P. Torminalis*) have two carpels only and simple leaves, those of the first-named species being covered on the under side by a soft white cotton.

The **mountain ash or rowan-tree** (*P. Aucuparia*), which grows to a moderate-sized tree, has pinnately compound leaves, corymbose flowers with three styles, and bright red fruits.

The **medlar** (*Mespilus germanica*) has large sessile solitary flowers, with long leafy sepals. The fruit, a pome, is large, and exhibits at the top the upper ends of the five cartilaginous carpels.

The **hawthorn** (*Cratægus*) differs from *Pyrus* in having a thick hard wall to the fruit instead of a thin one. The hard wall is enclosed in the fleshy receptacular cup. Carpels and styles one to three in number.

(vi) **Poterieæ.** This anomalous tribe consists of plants the flowers of which are often unisexual and devoid of a corolla; stamens and carpels few in number. Flowers often tetramerous.

The **lady's-mantle** (*Alchemilla vulgaris*) has palmately-lobed leaves, and numerous small greenish apetalous tetramerous flowers. There is one carpel which gives rise to an achenial fruit enclosed in the cavity of the receptacle, which is nearly closed at the top by a yellow perigynous disc (Fig. 183, VIII). There is an epicalyx.

The **great burnet** (*Poterium officinale*) and **salad burnet** (*P. Sanguisorba*) each have four sepals and no petals. The latter has polygamous flowers and indefinite stamens.

The **agrimony** (*Agrimonia*) has pentamerous yellow flowers, a corolla, and six to twelve stamens. The fruit is a burr adapted for dispersal by animals (Fig. 173, I, p. 334).

The plants in this order may usually be recognized by the stipulate leaves, regular flowers, indefinite perigynous stamens, and apocarpous pistil. They are distinguished from some *Leguminosæ* by the posterior odd sepal, and from *Saxifragaceæ* by the indefinite stamens and apocarpous pistil.

Floral formula of the rose, blackberry, *Potentilla*, strawberry, &c.,

K(5), C 5, A ∞, $G_{(\infty)}$; of the apple K (5), C 5, A ∞, $G\overline{5}$ (spuriously syncarpous).

** Order 13. **Leguminosæ.** The pea and bean family. This family, a very large one, is widely distributed, representatives being found over the greater part of the earth's surface. The British forms, which are included in about seventeen genera, all belong to the first of the three sub-orders into which the family is divided, e.g. *Papilioneæ*, *Cæsalpinieæ*, and *Mimoseæ*, and are characterized by the peculiar corolla and ten monadelphous or diadelphous stamens (Fig. 154, IV, V, p. 290). The leaves are nearly always compound (Fig. 227, p. 483); the flowers always lateral (never terminal); the pistil monocarpellary (Fig. 155, IV, p. 291); and the fruit is generally a legume (p. 320).

(i) **Papilioneæ.** The plants are trees, shrubs, or herbs, generally with stipulate compound leaves, and flowers in racemes or spikes, rarely solitary. The calyx is gamosepalous with the odd sepal *anterior* (not *posterior* as in *Rosaceæ*); the corolla is irregular and medianly zygomorphic, and consists of five petals, of which the posterior one is large, and forms the **standard** or **vexillum**: the two smaller lateral ones form the **wings** or **alæ**, and the other two are connate along their anterior margins, and form a boat-shaped body, the **keel** or **carina**, containing the stamens and pistil. The stamens form a single whorl, and are coherent by their filaments into one bundle (monadelphous), or nine are coherent and the other one free (diadelphous). The following are examples of British plants belonging to this sub-order:—

(*a*) *With monadelphous stamens* (Fig. 154, IV, p. 290).

Furze, gorse, or **whin** (*Ulex*). All the branches are small, and end in thorns. Most of the leaves are also reduced to thorns. Two species are usually recognized, a larger one (*U. europæus*), which begins flowering quite early in the spring, and a smaller one, the dwarf furze (*U. nanus*), which flowers later in the season, about August, and may often be seen on the moors of the west of England and elsewhere, flowering at the same time as the ling or heather (*Calluna*). The fruits (legumes) dehisce suddenly, and so scatter the seeds; this may be both seen and heard on any warm dry day in early autumn (see p. 333). The flowers are visited by insects for the sake of the pollen; no honey is formed.

Broom (*Cytisus*). With stiff, wiry, green angled branches and small compound leaves. There is a long curved style.

Genista. Much like the broom, but the leaves are simple, not compound.

The **rest-harrow** (*Ononis*). The flowers are pink, and the leaves generally pinnately trifoliate, with toothed leaflets resembling those of a *Trifolium.*

The **kidney-vetch** or **lady's-fingers** (*Anthyllis*). The plant is a herb with pinnate leaves, and heads of yellow or red flowers. The calyx is inflated, and encloses the fruit.

(*b*) *With diadelphous stamens* (Fig. 154, V, p. 290). Sometimes the upper stamen is only partially free.

The **clovers** (*Trifolium*), with ternate leaves and flowers in heads. The stipules are adnate (Fig. 227, II, s). The fruit contains from one to four seeds, and is usually indehiscent. This genus includes about twenty British wild species, some of which are very common. The **red** or **purple clover** (*T. pratense*) and the **white** or **Dutch clover** (*T. repens*) are cultivated.

The **vetches** and **tares** (*Vicia*) have pinnate leaves with many leaflets, frequently ending in leaf-tendrils. The flowers are often in racemes. The **common vetch** (*V. sativa*), with purplish flowers, is cultivated for forage, and the **hairy vetch** or **tare** (*V. hirsuta*), the **tufted vetch** (*V. Cracca*), the **bush vetch** (*V. sepium*), &c., are common plants.

The **common bean** is also a *Vicia*, and is supposed to have been produced by cultivation of a south European form.

The **wild peas** and **vetchlings** (*Lathyrus*) also have pinnate leaves, but the leaflets are few in number, generally two, and larger than in *Vicia.* The leaf-stalk commonly ends in a tendril (Figs. 5 and 7, pp. 15 and 16). Common forms are the **meadow pea** (*L. pratensis*), and the **tuberous pea** (*L. macrorrhizus*). The latter generally has two pairs of leaflets and no tendrils. The leaves of the **yellow vetchling** (*L. Aphaca*) have no leaflets, but two large stipules only and a slender branching tendril. The **sweet pea** is an exotic (Sicilian) species of *Lathyrus.*

The **medick** (*Medicago*) has a spirally-twisted, indehiscent, few-seeded legume. Leaves trifoliate. The flowers are generally yellow in colour. **Lucern** (*M. sativa*) is cultivated for cattle.

Melilot (*Melilotus*) has small yellow or white flowers in long, loose racemes. The pod is short, and contains one or two seeds only.

Lotus. Herbs usually with five leaflets, and yellow or reddish flowers in umbels. There is a trifoliate leafy bract below each

group of flowers. A common form is the **bird's-foot trefoil** (*L. corniculatus*). Five of the stamens have club-shaped ends; these stamens shed their pollen early, and their function is to push the shed pollen out of the end of the keel when the wings are depressed by an insect.

The **bird's-foot** (*Ornithopus*) has pinnate leaves. The pods somewhat resemble bird's claws; they are curved, constricted between the seeds, and pointed.

The **common sainfoin** (*Onobrychis*) is a pretty herb with pinnate leaves, and spikes of pink flowers. The fruit is one-seeded, and indehiscent. It is cultivated for forage.

Edible peas are the seeds of *Pisum sativum*, which is closely related to *Lathyrus*.

The **scarlet runner** and **kidney** or **French beans** are species of *Phaseolus*.

The **laburnum** is a species of *Cytisus*.

Robinia, the so-called **acacia** or **false acacia**, also belongs to this sub-order.

(ii) **Cæsalpinieæ**. Flowers *not papilionaceous*; the five petals nearly regular (really medianly zygomorphic), imbricate in the bud; stamens generally *free*, and ten in number; fruit indehiscent, and frequently divided by transverse septa. Mainly tropical.

The **locust** or **carob-bean** is the fruit of *Ceratonia*; **senna** consists of the leaflets of species of *Cassia*; the **Judas-tree** is *Cercis siliquastrum*, and the **logwood-tree** is *Hæmatoxylon*.

(iii) **Mimoseæ**. This tribe is also mainly tropical in distribution. The flowers are regular, and valvate in the bud, with numerous usually free stamens; often crowded in heads or spikes. Fruit often transversely septate.

The genus **Acacia** (Fig. 227, IV, p. 483) is represented by numerous species in Australia, Africa, and Asia; many species are cultivated for their beauty. The Australian forms often show flattened petioles or phyllodes, with or without a terminal bipinnate lamina. They yield gum-arabic, wattle-gums, &c.

The **sensitive plants** (*Mimosa*) have irritable leaflets which respond to touch, shaking, and to darkness. The leaflets of the compound pinnate leaves fold together under the influence of these stimuli (p. 474, and Fig. 227, p. 483).

Floral formula of the *Papilioneæ*, K (5), C 5, A (10) or (9) + 1, $G\underline{1}$.

Order 14. **Saxifragaceæ.** The saxifrage family. An extensive family, which is represented by trees, shrubs, and herbs, with exstipulate

leaves and regular perigynous or epigynous flowers. Stamens definite in number and in one or two whorls; carpels few, syncarpous, but often free above; styles free.

The **saxifrage** (*Saxifraga*), of which there are several wild species in Britain, has (generally) alternate leaves, flowers in racemose cymes, two whorls of stamens, and a bicarpellary ovary, the carpels of which are often free above (Fig. 155, II, p. 291). Many of the forms live at high altitudes; those inhabiting limestone districts often have 'chalk-glands' and 'water-stomata' on their leaves (Fig. 207, p. 436). A chalk-gland consists of a solid mass of cells close to the margin of the leaf; it is continuous below with the vascular bundle and above with the water-stomata, by which water containing calcium carbonate escapes, leaving a deposit along the edge of the leaf. *Saxifraga umbrosa* is the **London pride.**

The **golden saxifrage** (*Chrysosplenium*) is a small delicate herb, with tetramerous apetalous flowers, and found in moist shady places.

The so-called '**Spiræa japonica**' belongs to this order and to the genus *Astilbe.* (The true *Spiræa* belongs to the Rosaceæ.)

The **grass of Parnassus** (*Parnassia*), which occurs in bogs and other swampy places, has radical entire leaves, and flowers in which five of the ten stamens are represented by glandular staminodes, each bearing a tuft of globular-headed filaments.

Hydrangea has epigynous flowers, with large petaloid sepals and three to five carpels. The marginal flowers of each inflorescence are neuter—in the cultivated *H. hortensis*, all are so.

Philadelphus (**mock orange** or '**Syringa**'), *Deutzia*, &c., are cultivated.

The tribe **Ribesieæ** includes the **gooseberry** and **currants** of our gardens. They are shrubs with racemes or solitary flowers, which are epigynous and generally pentamerous. Stamens five; carpels two; ovary unilocular, with two parietal placentæ; fruit a berry in which much of the pulp is composed of the succulent and thick testas of the seeds (Fig. 169, I, p. 323).

Ribes Grossularia is the **gooseberry.** The leaf-base is produced into thorns. *R. rubrum* is the **red currant**, *R. nigrum* the **black currant.** *R. sanguineum*, an American species, is the '**flowering currant**' of our gardens.

The plants in this order are recognized by the exstipulate leaves, perigynous or epigynous flowers, definite stamens, syncarpous ovary, and free styles.

Floral formula of *Saxifraga*, K (5), C 5, A 5+5, $G\underline{(2)}$; of *Ribes*, K (4-5), C 4-5, A 5, $G\overline{(2)}$.

Order 15. **Crassulaceæ.** The stonecrop family. The plants in this order generally inhabit dry situations, such as stone walls, roofs, &c. They have simple exstipulate succulent leaves, and regular flowers in terminal cymes; the pistil is apocarpous and consists of as many carpels as there are sepals and petals; the fruit is an etærio of follicles.

The **stonecrops** (*Sedum*) include about ten British species. The flowers are usually pentamerous with two whorls of obdiplostemonous stamens. The petals are free. A very common form is the **wall-pepper** (*S. acre*) found on walls and rocks. The **orpine or livelong** (*S. Telephium*) is a much larger plant, with purple flowers and flat leaves. The **rose-root** (*S. rhodiola*) of the northern counties has dicœcious tetramerous flowers. Some exotic species of *Sedum* are cultivated.

The **pennywort** (*Cotyledon umbilicus*), a form with fleshy and more or less peltate leaves, occurs on walls, &c., and is very common in the west of England. The flowers are pentamerous and the corolla gamopetalous.

The **house-leek** (*Sempervivum*) is commonly seen on cottage roofs. The fleshy leaves are in spirally arranged rosettes. It produces short offsets or stolons, each of which produces a bud at its end and grows into a new plant. The sepals, petals, and carpels are numerous, generally ten to twelve in number, and the stamens are twice as many, though some of the latter may become aborted or changed into carpels.

The cultivated *Crassula* (Fig. 155, I, p. 291), *Echeveria*, &c., also belong to this order; they are all succulents.

The plants in this order are recognized by the fleshy leaves, regular flowers, and apocarpous pistil composed of as many carpels as there are sepals and petals. Floral formula of *Sedum* is generally K (5), C 5, A 5+5, $G\underline{5}$.

Order 16. **Onagraceæ.** The willow-herb family. Herbs or shrubs with simple exstipulate leaves and regular dimerous or tetramerous epigynous flowers. Sepals with valvate æstivation; stamens generally in two whorls and inserted on the calyx tube; gynæcium syncarpous with numerous ovules on axile placentæ.

The willow-herbs (*Epilobium*) are represented by many British species, some of which have large and handsome purple or pink

flowers. The flowers are generally tetramerous throughout; the fruit is a long narrow capsule, which splits septifragally into four valves to liberate the numerous hairy seeds (Fig. 172, II, p. 332). The **rose-bay** (*E. angustifolium*) and the **great willow-herb** (*E. hirsutum*) are widely distributed handsome species; in the former the flowers are somewhat irregular in form. In *E. angustifolium* the stigma is four-lobed, but it does not unfold until long after the dehiscence of the anthers, showing that the plant is markedly protandrous. The nectary lies within the bases of the stamens (cf. *Umbelliferæ*). Common smaller forms of *Epilobium* are the **broad-leaved epilobe** (*E. montanum*) and the **square epilobe** (*E. tetragonum*), the latter with ridges on the stem descending from the margins of the leaves.

The **evening primrose** (*Œnothera*) has large yellow tetramerous flowers in a long terminal spike. The fruit, a capsule, is not as long and narrow as in *Epilobium*, and the seeds have no hairy tuft.

The **enchanter's nightshade** (*Circæa*) is common in woods, &c. The flowers are in racemes and are dimerous; they have only two stamens, and the two-seeded globular capsule is covered with small hooked hairs.

Clarkia and *Fuchsia* are American forms: in the latter genus the fruit is a berry.

The order is readily recognized among the Calycifloræ by the regular tetramerous or dimerous flowers and the inferior ovary. Floral formula of *Epilobium* and *Œnothera*, K (4), C 4, A 4+4, G $\underline{(4)}$; of *Circæa*, K 2, C 2, A 2, G $\underline{(2)}$. See floral diagram, Fig. 157, I, p. 293.

* Order 17. **Cucurbitaceæ.** The gourd family (Fig. 185). The only British plant belonging to this order is the **white bryony** (*Bryonia dioica*), but many others are cultivated for the sake of their fruits, such as the **cucumber, vegetable marrow, melon**, &c.

The plants are climbing herbs with alternate palmately-lobed leaves and unisexual flowers; corolla often gamopetalous; five stamens, four of which commonly cohere in pairs so that they appear to be only three in number; sinuous anthers and dehiscence; ovary inferior and really unilocular, but becoming spuriously multilocular, with axile placentæ; fruit, an inferior berry with a thick pericarp, often of great size (Fig. 169, II, p. 323).

The **white bryony** (*Bryonia dioica*) has extra-axillary tendrils growing out at the sides of the leaves, and concerning the morphological nature of which there is much difference of opinion (supra, p. 14). These tendrils sometimes branch and are generally regarded

as modified leaves (Fig. 185, I). This plant is diœcious; the fruit is a globular red berry.

Many of the plants in this order are covered with rough hispid hairs.

The plants in this order may be recognized by the unisexual (monœcious or diœcious) flowers, and by the foliage and tendrils. Floral formula of *Bryonia*, ♂ K (5), C (5), A (5 fused into 3), G 0; ♀ K (5), C (5), A 0, $G\overline{(3)}$.

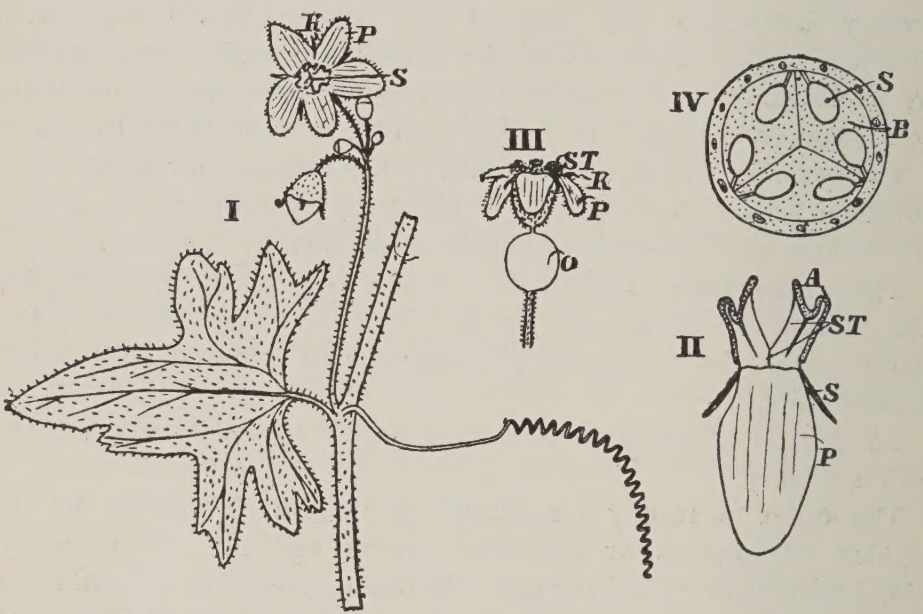


FIG. 185. *Cucurbitaceæ*. I. Male plant of the White Bryony (*Bryonia dioica*), showing palmately lobed leaf, tendril, and male flowers. K=sepals; P=petals; S=stamens. II. Two of the stamens with adherent petal from I. The stamens (ST) are fused at the base. A=sinuous anther; P=petal; S=sepals. The stamens are seen from the outside; the petal has been pulled downward. III. Female flower from female plant of *Bryonia*. K=sepals; O=the inferior ovary; P=petals; ST=stigmas. IV. Transverse section of ovary. S=seeds; the space B is entirely filled with succulent tissue. The placentation appears to be parietal, but is really axile, as the placentæ after being folded inward turn outwards again.

** Order 18. **Umbelliferæ.** A very large and important family which is widely scattered over the surface of the globe and represented in Britain by between thirty and forty genera, all of which are herbaceous. The stems are generally hollow (fistular) and the leaves much divided and sheathing at the base; the inflorescence is typically a compound umbel, with or without an involucre at the base of the main umbel, or involucels below the partial umbels (supra, p. 301); flowers regular and pentamerous; calyx often very small; corolla epigynous and regular, sometimes irregular in those flowers which

form the margin of the umbel; ovary bilocular, with an epigynous disc (nectary) formed of the bases of the free styles; fruit, a cremocarp (a variety of schizocarp) splitting into two one-seeded portions, or mericarps, which remain suspended from a slender carpophore (Fig. 167, I, p. 319). The fruit is marked with longitudinal ridges enclosing vascular bundles; in the furrows between the ridges lie a number of oil-ducts or receptacles termed **vittæ**. Seeds albuminous.

The numerous forms in this order are classified in a very artificial manner, mainly on details connected with the fruit—whether compressed or cylindrical, the prominence and number of its ridges, vittæ, &c. Details of this classification may be found in a good Flora such as Hooker's, and to use it the fruits must be examined in a ripe condition. Here only some of the commonest genera and species will be mentioned.

(i) *With flowers in simple umbels or heads.*

Marsh pennywort or **white-rot** (*Hydrocotyle vulgaris*). An aquatic or marsh plant with orbicular peltate leaves and minute flowers. The fruit is laterally compressed.

Sanicle (*Sanicula europæa*) is a common plant in woods. The leaves are palmately divided, and the white flowers occur in small umbels or heads. It is readily distinguished by the fruits, which are small burrs covered with hooked prickles and crowned by five stiff calyx teeth.

Sea-holly (*Eryngium maritimum*). A fairly common stiff plant, with broad simple leaves provided with coarse prickly teeth. The flowers are blue in colour, and are arranged in compact heads.

(ii) *With flowers in compound umbels.*

Celery (*Apium graveolens*) occurs in marshy places near the sea; it has pinnate leaves, of three or five cut leaflets, and lateral umbels of white flowers. The cultivated celery is a variety of this species. The **procumbent apium** (*A. nodiflorum*) is a very common marsh and ditch plant. The umbels are mostly lateral.

The **goutweed** (*Ægopodium*). This plant grows to a height of one or two feet, and the large terminal umbels of flowers have no involucres.

The **caraway** (*Carum Carui*) is cultivated for its carpels, or cocci, which are known as caraway seeds. **Parsley** (*Carum petroselinum*) is cultivated, but it may also be found wild in parts of northern and western England.

The **burnet saxifrage** (*Pimpinella Saxifraga*) has pinnate leaves and flowers without involucres.

The **hare's-ear** (*Bupleurum rotundifolium*) is sometimes found in cornfields in chalky soils. It is easily distinguished by its perfoliate leaves, i. e. the leaves appear to be pierced by the stem, and by its large partial involucres, consisting of yellowish leaves which are much longer than the flowers.

The **water-dropwort** (*Œnanthe Fistulosa*) is common in wet meadows and marshes, as is also the **hemlock water-dropwort** (*Œ. crocata*). The former has a tubular stem and leaves. Only the central flowers of the compound umbels are fertile, and these are nearly sessile; the outer flowers have larger petals, but are barren and pedicellate. These plants are very poisonous.

Fool's parsley (*Æthusa Cynapium*) is a common weed. The partial involucres consist of long and narrow leaves which turn downward. There is no general involucre.

The **common fennel** (*Fœniculum vulgare*). The leaves are very finely divided into narrow segments. The flowers are yellow and are arranged in large terminal umbels.

The **samphire** (*Crithmum maritimum*) occurs close to the sea. The stems and leaves are very thick and succulent; the flowers are yellow.

Wild angelica (*Angelica sylvestris*) is a common tall weed in wet places. The leaves are bipinnate; the flowers have both general and partial involucres, and the fruit is bordered by two thin wings, which are distinct before the fruit is ripe and before the carpels separate. The **garden angelica** is a cultivated form belonging to the same genus.

The **parsnip** (*Pastinaca sativa*). This plant is generally a biennial and forms a tap-root, well seen in an enlarged form in the garden variety. The flowers are small and yellow.

Cow-parsnip or **hogweed** (*Heracleum Sphondylium*) is a very common meadow plant. It is a large hairy plant, four to six feet in height, with pinnate leaves and large umbels of white flowers. The outer petals of the umbels are much larger than the others, and so make the whole inflorescence more conspicuous than would otherwise be the case.

The **shepherd's needle** (*Scandix Pecten*) is easily distinguished by its long narrow fruits, which may attain two inches in length. The greater part of the length of the fruit is taken up by the smooth

flattened beak, which is compared to the tooth of a comb (hence the plant is known also as **Venus's comb**).

The **wild chervil** (*Chærophyllum sylvestre*) and the **rough chervil** (*C. temulum*) are common.

The **knotted caucalis** (*Caucalis nodosa*) and **hedge-parsley** (*C. Anthriscus*) have umbels of but few rays, and bristly fruits (small burrs).

The **carrot** (*Daucus Carota*) is common, especially near the sea. The leaves are cut into narrow segments; the bracts are divided into three or five narrow lobes (pinnatifid), and after flowering the pedicels of the outer flowers of the umbel bend over inwards, so that the umbel becomes concave and something like a bird's nest. The fruit is covered with prickles, and the whole plant has a strong odour when bruised. The central flower (or flowers) of the umbel is often coloured red or purple, while all the outer ones are white.

Hemlock (*Conium maculatum*). The real hemlock (many species of umbelliferous plants are commonly given this name) is a tall, graceful plant, with very much divided pinnate leaves; the slender stem is smooth and glabrous; the umbels of small white flowers are terminal, and consist of ten to fifteen rays; there are general and partial involucres, and the bracts of the latter are all turned to the outside of the umbel. Hemlock is very poisonous.

The plants in this family may be identified generally by the much-divided leaves with sheathing bases, the umbellate inflorescence, the pentamerous flowers, inferior ovary, and characteristic fruit. Floral formula, K 5, C 5, A 5, $G\overline{(2)}$. The calyx is often small, and sometimes absent.

Series C. Gamopetalæ.

(*a.*) Ovary superior.

Order 19. **Ericaceæ.** The heath family (Fig. 186). A large family, most abundant in temperate and cold regions. The British forms are generally small woody plants, with tough wiry stems and small evergreen entire leaves, and are found on moors, &c.

The sepals may be free or coherent, and are four or five in number; the stamens, which are in two whorls, are nearly or quite free from the corolla; the anthers generally open by pores near to or at the top, and they are commonly provided with tailed appendages at the base (Fig. 186, II); the four- or five-celled ovary is superior (except in

Vaccinium), and is surrounded by a glandular disc; the fruit is a capsule or a berry. The British forms belong to about eight genera, of which *Erica*, *Calluna*, and *Vaccinium* are common. The other British genera are *Arctostaphylos* (**bearberry**), *Andromeda*, *Loiseleuria*, *Menziesia*, *Pyrola* (**wintergreen**), and *Monotropa*.

The genus *Erica* (the **heaths**) include a number of social plants of which there are about five British species. Common forms are the **cross-leaved heath** (*E. Tetralix*), with 'rolled' leaves in fours (see p. 458), and the **bell-** or **Scotch heather** (*E. cinerea*), with numerous purple flowers in racemes. *Calluna vulgaris* (**the ling**) is a very abundant form, with small opposite decussate 'rolled' leaves (see Fig. 220, IV, V, p. 459) and pink or sometimes nearly white flowers in racemes.

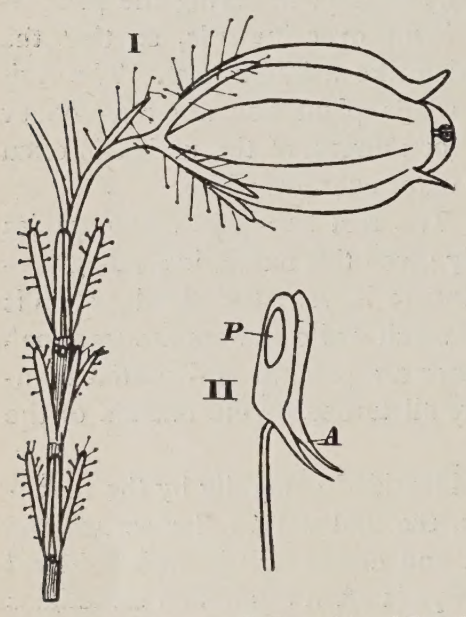


FIG. 186. *Ericaceæ*. I. Cross-leaved Heath (*Erica Tetralix*). The leaves are in whorls of four and each is rolled back (see p 458). II. A single stamen of the same. A=the tailed appendages of the anthers; P=pore through which the pollen escapes.

Vaccinium includes four British species. *V. Myrtillus* is the **bilberry** or **whortleberry**; *V. uliginosum* is the **bog vaccinium** of the highlands of North Britain; *V. Oxycoccos* is the **cranberry**; and *V. Vitis-idæa* the **red whortleberry** or **cowberry**. Most of these forms are found on elevated heaths and moors, and in woods, and they differ from the other forms in the order in having an inferior ovary, and consequently epigynous corolla and stamens; the fruit is a berry.

The genus *Pyrola* (**wintergreen**) includes several British species which differ from the ordinary *Ericaceæ* in habit and foliage. The plants are herbs, not shrubs, and bear radical roundish leaves; they are found in woods and moist shady places, where they live as partial saprophytes (p. 423). Many of the ordinary heaths are partial saprophytes.

Monotropa Hypopitys (**yellow bird's-nest**) is also a herb, but its leaves are reduced to small scales covering the somewhat succulent stem which develops into a raceme of brownish flowers. The whole

plant somewhat resembles *Orobanche*, and it is probably a root parasite.

Arbutus (the **strawberry-tree**) is found in parts of Ireland. It is a tall shrub or tree with alternate evergreen leaves, and a baccate fruit somewhat resembling a strawberry in appearance, though not in flavour. The flowers are pentamerous.

The **rhododendrons**, **azaleas**, and **kalmias** are cultivated European, Asiatic, and American forms. The anthers have no appendages, and the fruit dehisces sepiticidally, not loculicidally, as in *Erica*. In Australia the *Ericaceæ* are replaced by the closely allied *Epacridaceæ*, some of the forms of which are commonly cultivated in this country.

The order may generally be recognized by the prevailing shrubby habit, hypogynous or epigynous stamens, porous dehiscence of the anthers and appendages of the latter. Floral formula of *Erica*, K 4, C (4), A 4+4, $G\underline{(4)}$; of *Vaccinium*, K (4–5), C 4–5, A 8–10, $G\overline{(4-5)}$.

** Order 20. **Primulaceæ.** The primrose family. Comprises about twenty genera, inhabiting especially high altitudes in the northern hemisphere. They are herbs with alternate or opposite simple, or rarely compound, exstipulate leaves, regular pentamerous flowers, with the epipetalous stamens opposite to the corolla lobes; free central placentation, and a single style with capitate stigma (Fig. 155, III, p. 291); fruit capsular, dehiscing by teeth, or, occasionally, transversely.

The genus *Primula* includes the **primrose** and **cowslip**, which have radicle leaves and umbellate inflorescences. In the primrose the common peduncle is very short, so that the umbellate character of the inflorescence is not readily apparent. The flowers are dimorphic (p. 310). The antipetalous position of the stamens is explained as due to the suppression of an outer whorl, which is represented in some genera (e.g. *Soldanella*) by staminodes. The stems of the closely related **auriculas** are polystelic. The **polyanthuses** of our gardens are cultivated varieties of the primrose.

The **cyclamen** has reflexed petals.

The **yellow loosestrife** (*Lysimachia vulgaris*) has whorled leaves and flowers in terminal panicles.

The **water-violet** (*Hottonia*) has submerged pinnatifid leaves and handsome whorled flowers on aërial peduncles.

The **scarlet pimpernel** (*Anagallis arvensis*) has opposite leaves and a capsule (pyxidium), which dehisces transversely.

The **sea-milkwort** (*Glaux maritima*) has a petaloid calyx but no corolla.

The order is recognized among British Gamopetalæ by the free central placentation, epipetalous stamens opposite the corolla lobes, and single style and stigma. Floral formula (generally), K (5), [C (5), A 5], $G\underline{(5)}$.

* Order 21. **Gentianaceæ.** The gentian family. A large order of glabrous herbs with bitter juice and opposite exstipulate entire leaves. The inflorescence is usually a dichasial cyme; the flowers are regular; the stamens epipetalous and alternating with the petals; and the ovary unilocular with two parietal placentæ and many ovules.

The **gentian** (*Gentiana*) is represented by several British species, with blue pentamerous or tetramerous flowers and a bilobed stigma.

The **common centaury** (*Erythræa*) has pink flowers and a capitate stigma.

The **perfoliate yellow-wort** (*Chlora*) has a yellow rotate corolla with eight lobes. Leaves perfoliate.

The **bogbean** or **buckbean** (*Menyanthes*) is an aquatic, with compound trifoliate leaves and white flowers.

The order is recognized by the regularly alternating pentamerous flowers, the contorted æstivation of the corolla, the bicarpellary ovary with parietal placentæ, and the bitter juice. Floral formula (generally), K (5), [C (5), A 5], $G\underline{(2)}$.

Order 22. **Oleaceæ.** The olive family. A small order of trees and shrubs, including two British species, the **common ash** (*Fraxinus*) and the **privet** (*Ligustrum*), and some commonly cultivated exotic forms.

The leaves are generally opposite, and either simple or pinnately compound; the flowers are regular, generally hermaphrodite and tetramerous; stamens and carpels always two in number, alternating, the former attached to the base of the corolla-tube; ovary bilocular, with two ovules in each loculus; style simple.

The **privet** (*Ligustrum*) is a shrub with simple leaves and a black baccate fruit. The small white flowers are arranged in panicles.

The **common ash** (*Fraxinus excelsior*, Figs. 151, I, II, and 167, V, pp. 282, 319) has pinnate leaves and small achlamydeous polygamous flowers. Fruit a samara. The **manna ash** (*F. ornus*), a south European species, possesses flowers with both calyx and corolla, and is sometimes called the 'flowering ash.'

The **lilac** (*Syringa vulgaris*) and *Forsythia* have capsular fruits.

The **olive** (*Olea*) of southern Europe, Greece, Syria, &c., has a drupaceous fruit with an oily mesocarp yielding one of the most valuable of oils.

The **jessamine** (*Jasminum*) differs from the other genera mentioned in the possession of pentamerous (not tetramerous) flowers, two median (instead of lateral) stamens, and imbricate (not valvate) petals. They are climbing shrubs, and several species are cultivated.

The *Oleaceæ* may generally be recognized by their opposite leaves and tetramerous flowers with two stamens. Floral formula (generally), K (4), [C (4), A 2], G$\underline{(2)}$.

*Order 23. **Convolvulaceæ.** The convolvulus family. A large order which abounds in the tropics. The plants often climb on others by means of their twining stems. Of the 800 species included in the order about 300 belong to the single genus *Ipomœa*, some species of which are commonly cultivated. The family includes only two British genera, the **bindweed** (*Convolvulus*) and **dodder** (*Cuscuta*).

The leaves are alternate and exstipulate; the flowers regular and pentamerous with free sepals; petals contorted in the bud; pistil of two median carpels forming a bilocular ovary with two ovules in each cell; fruit generally a capsule splitting septifragally and loculicidally into four valves, or sometimes dehiscing transversely.

The **bindweeds** (*Convolvulus*) are prostrate or twining herbs with a campanulate corolla, and bracteoles; the latter may be small and at some distance below the calyx, or large and leafy, forming a kind of involucre under the flower. The latter forms are often described as a distinct genus (*Calystegia*), of which the **larger bindweed** (*Calystegia sepium*) with its large pure white flowers is a common example.

The other British genus, the **dodder** (*Cuscuta*), consists of climbing parasites destitute of chlorophyll. It commonly attacks clover, flax, heath, nettles, hops, &c. (see p. 422).

This order is generally recognized by the climbing habit; free sepals; contorted æstivation of the petals; and bilocular ovary. The plants generally contain some milky latex. Floral formula of *Convolvulus*, K 5, [C (5), A 5], G$\underline{(2)}$.

Order 24. **Solanaceæ.** The nightshade family (Fig. 187). A large order common in all the warmer regions of the globe, and including three British genera, *Solanum*, *Atropa*, and *Hyoscyamus*. Most of the plants in this order are more or less poisonous, as they contain powerful narcotics; some, however, such as the potato-plant, yield valuable articles of food.

The plants are usually herbs with simple exstipulate alternate leaves and cymose pentamerous regular flowers. The calyx is generally persistent; the ovary is bilocular with many ovules on axile placentæ, and the fruit is a capsule or berry. Some of the anthers may be sterile.

The genus *Solanum* includes forms in which the anthers are syngenesious and dehisce by spores. *S. dulcamara* is the common **woody nightshade**, the berries of which are red; *S. nigrum* is the **black nightshade**, with white flowers and black berries. The **potato-plant** (*S. tuberosum*) was originally introduced from South America.

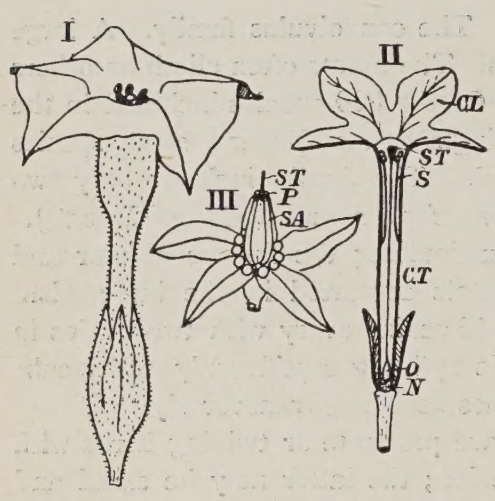


FIG. 187. *Solanaceæ*. I. Flower of Tobacco-plant (*Nicotiana*). II. Flower of another kind of Tobacco-plant, in section. CL = corolla limb; CT = corolla tube; N = nectary; O = ovary; S = epipetalous stamens; ST = bilobed stigma. III. Flower of Woody Nightshade (*Solanum*). P = pores through which pollen escapes; SA = syngenesious anthers; ST = stigma.

The **deadly nightshade** (*Atropa Belladonna*) has a campanulate corolla and black poisonous berries about the size of a small cherry, and surrounded by the persistent calyx. The drug *atropine* is obtained from this plant.

The **winter cherry** (*Physalis*) has an edible berry surrounded by the inflated red caylx.

The **common henbane** (*Hyoscyamus*) has a capsular fruit with transverse dehiscence. It is poisonous.

Other well-known plants belonging to this order are the **Chili peppers** (*Capsicum*), the **tomato** (*Lycopersicum*), **tobacco** (*Nicotiana*), *Petunia*, the **thorn apple** (*Datura*) with a prickly capsule opening in four valves and spuriously tetralocular, &c.

The order may generally be recognized by the regular pentamerous flowers with a bilocular ovary and many ovules on axile placentæ. Floral formula, K (5), [C (5), A 5], $G\underline{(2)}$.

Order 25. **Boraginaceæ.** The borage family (Fig. 188). A large family of herbs belonging mainly to the cooler parts of the northern hemisphere and represented in Britain by about ten genera, some of which are very rare.

The plants are usually very rough with stiff hairs; the leaves are

simple, alternate, exstipulate, and entire; the inflorescence a branched scorpioid cyme (supra, p. 302); the flowers regular and pentamerous, with scaly appendages to the corolla at the junction of the tube with the limb; ovary of two carpels which become spuriously quadrilocular in consequence of constriction along the midrib of

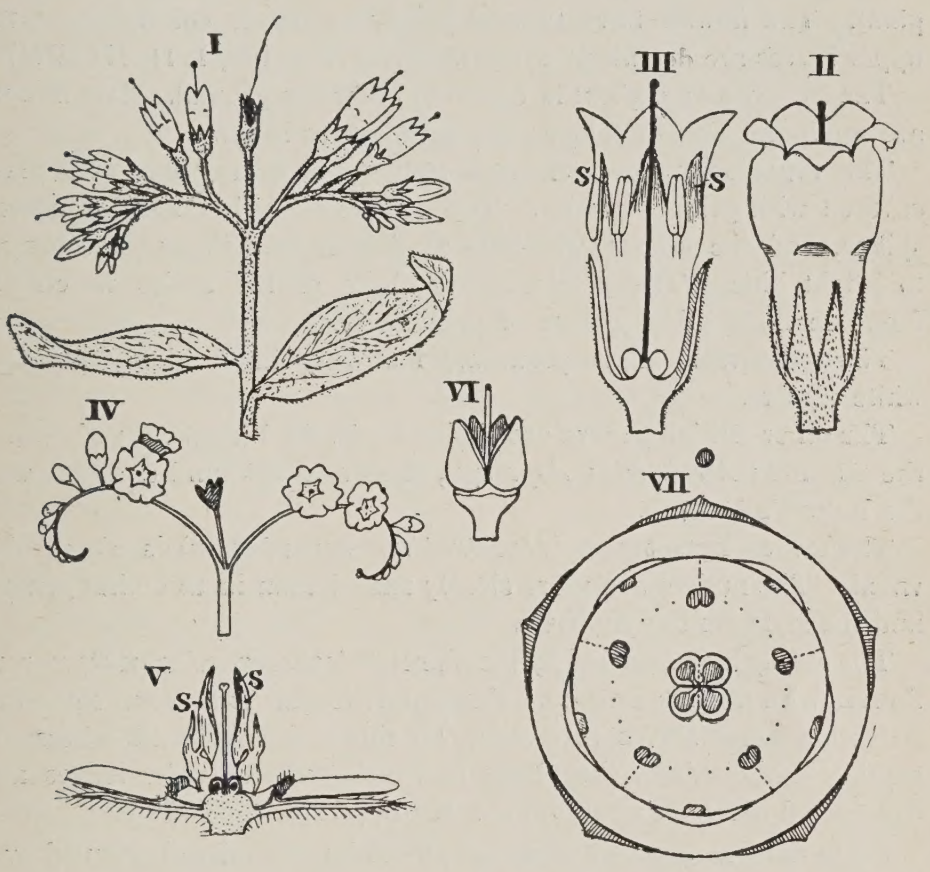


FIG. 188. *Boraginaceæ*. I. The Comfrey (*Symphytum officinale*), showing the characteristic inflorescence. II. Single flower of the same. III. The same in vertical section. S, S = scaly outgrowths from the corolla. IV. Inflorescence of the Forget-me-not (*Myosotis*). V. Flower of the Borage (*Borago*) in vertical section. S, S = two of the peculiar stamens which form an erect cone in the centre of the flower. Note the gynobasic style, i. e. arising from the base of the ovary. VI. Fruit of *Myosotis*. VII. Floral diagram of the Comfrey. The dorsal constrictions of the carpels are shown by the dotted lines.

each carpel; style arising from between the carpels (gynobasic); fruit consisting of four one-seeded nutlets, as in the Labiatæ.

The genus *Myosotis* (Fig. 188, IV) includes several common British forms as well as some cultivated exotics. *M. palustris* is the **forget-me-not**. Other common wild forms are the **field myosotis** (*M. ar-*

vensis) and the **changing myosotis** (*M. versicolor*), so called because the yellow corolla changes to blue as it fades.

The **common borage** (*Borago officinalis*) is much like a large rough forget-me-not. The blue corolla is rotate and the anthers form an erect cone in the centre of the flower (Fig. 188, V).

The **comfrey** (*Symphytum officinale*) is a large handsome common plant. The flowers have tubular yellow or purple corollas, and the upper leaves are decurrent along the stem (Fig. 188, I, II, III, VII).

The **bugloss** (*Lycopsis*) is common on waste ground. The flowers are small and blue in colour; the corolla-tube is bent.

The **viper's bugloss** (*Echium vulgare*) is a very handsome plant covered with prickly bristles. The flowers occur in one-sided curved spikes, and the colour, which is at first a reddish purple, changes to bright blue. The petals are destitute of the scales which are found in most other genera of this family.

The **gromwell** (*Lithospermum*) has very hard, highly polished white nutlets.

The other British genera are *Pulmonaria*, the **lungwort**; *Anchusa*, the **alkanet**; *Mertensia*; *Asperugo*, the **madwort**; and *Cynoglossum*, the **hound's-tongue.**

The **sweet heliotrope** (*Heliotropium peruvianum*) is often cultivated. The nutlets are more closely united than in the other genera, and the style is not gynobasic.

The family is recognized by the alternate leaves, regular pentamerous flowers with five stamens, and characteristic fruit of four nutlets. The latter character serves to distinguish this order from all others excepting the *Labiatæ*, the plants of which have opposite leaves and irregular flowers. Floral formula, K (5), [C (5), A 5], $G\underline{(2)}$.

** Order 26. **Scrophulariaceæ.** A large family distributed over the greater part of the globe, but most abundant in temperate or elevated regions. The plants are generally herbs, sometimes shrubs, with either alternate or opposite, simple, exstipulate leaves; some are root parasites. The kind of inflorescence varies; the flowers are generally pentamerous but with reduction in the androecium and gynæcium; calyx persistent; corolla often zygomorphic and bilabiate, sometimes nearly regular and rotate (*Veronica*); stamens typically four in number and didynamous, the posterior stamen being aborted, but sometimes five are present (*Verbascum*) or only two (*Veronica*); pistil of two carpels with many ovules on axile placentæ (Fig. 156, II, p. 292); fruit generally a capsule (Fig. 168, III, p. 321).

The **figwort** (*Scrophularia nodosa*) has opposite leaves and dingy, nearly globular, flowers. *S. aquatica* is the **water figwort.** Both species are common.

The **foxglove** (*Digitalis purpurea*) is a tall hedge plant with alternate leaves and conspicuous terminal racemes of open flowers. The genus is cultivated.

The genus *Linaria* includes several common British species as well as some cultivated forms. The flower has a two-lipped closed (personate) spurred corolla. *L. vulgaris* is the common **yellow toadflax,** which has its flowers in short racemes. *L. Cymbalaria,* the **ivy-leaved toadflax,** is a trailing perennial commonly found growing on walls.

The **snapdragon** (*Antirrhinum*) differs from *Linaria* in the absence of the long spur (Fig. 228, VI, p. 485). Two British species are found, the **great snapdragon** (*A. majus*), with showy flowers, and the **lesser snapdragon** (*A. Orontium*), a smaller plant with smaller flowers.

The **musk** (*Mimulus*) occurs wild in some wet places (see p. 474).

The **mullein** (*Verbascum*) has coarse alternate leaves and five stamens. The corolla is rotate and nearly regular, with a very short tube.

The **speedwell** (*Veronica*) has a rotate open zygomorphic flower. The lobes of the corolla are reduced to four by the union of the two posterior petals into one broad one. Only the two posterior stamens are developed and the loculicidal capsule contains only a few seeds. The flowers are in terminal or axillary spikes or racemes, sometimes solitary and axillary. There are many British species.

The genera *Bartsia, Euphrasia* (**eyebright**), *Rhinanthus* (**yellow rattle**), *Melampyrum* (**cow-wheat**), and *Pedicularis* (**red rattle**), are all root parasites (see p. 423). The leaves are opposite (except *Pedicularis*) and possess some chlorophyll, so that they are only partial, not complete, parasites. They attach themselves to the roots of grasses and other plants by means of **haustoria**[1] developed on the roots. Most of these genera have only four sepals, a two-lipped corolla, and four stamens.

Commonly cultivated genera include *Pentstemon, Calceolaria, Mimulus* (including the common **musk** and the '**monkey flowers**'), *Paulownia imperialis* (the so-called **vanilla tree,** from Japan), *Browallia,* &c.

[1] Haustoria are the root-like processes containing vascular tissue by which many parasitic plants absorb their nutriment from the host (infra, p. 422).

In most cases the plants in this order may be recognized by the zygomorphic and generally two-lipped corolla, the didynamous stamens, and many-seeded bilocular ovary with axile placentation. Typical floral formula, K (5), [C (5), A 4], G$\underline{(2)}$.

Order 27. **Plantaginaceæ.** The plantain family. A small order of herbs with rosettes of simple exstipulate leaves and flowers in spikes or heads. The flowers are sometimes unisexual and monœcious (*Littorella*), and are apparently tetramerous, having four sepals, four petals, four stamens, and, generally, two carpels. The tetramerous structure of the flowers is best explained by analogy with *Veronica*, the posterior sepal and stamen being suppressed and the two posterior petals fused into one. The ovary and the fruit, which is a capsule, are generally two-celled, with one or a few ovules, or seeds, in each loculus; the dehiscence of the fruit is transverse.

The **plantains** (*Plantago*) are very common weeds, with hermaphrodite flowers. The **greater plantain** (*P. major*) has broad-stalked ribbed leaves and green flowers in a long slender spike. The ripe spikes are used as food for birds. The **hoary plantain** (*P. media*) has ovate sessile leaves, which lie on the ground, and a spike forming one-seeded capsules. The **ribwort plantain** (*P. lanceolata*), with narrow leaves and a short spike, is also common. The other British species are the **sea-plantain** (*P. maritima*) and the **buck's-horn plantain** (*P. coronopus*).

The other British genus (*Littorella*) is represented by a single species, the **littorel** (*L. lacustris*), a small perennial found on the muddy or sandy margins of pools. The plant is monœcious and the fruit a one-seeded indehiscent nut.

The genus *Plantago* is recognized by the spicate inflorescence, tetramerous flowers, scarious corolla and capsular fruit. Floral formula (generally), K 4, [C (4), A 4], G$\underline{(2)}$.

** Order 28. **Labiatæ.** The dead-nettle family (Fig. 189). One of the largest orders, and spread all over the globe, but especially numerous in the Mediterranean region. The plants are generally herbs, with square stems and opposite decussate simple exstipulate leaves, and flowers in cymes forming verticillasters in the axils of the leaves (Fig. 164, VI, VII, p. 303). The flowers are medianly zygomorphic and bilabiate (Fig. 189), pentamerous, but with reduction of the stamens to four or occasionally two; carpels two, median.

The calyx is persistent and often more or less two-lipped; the corolla is bilabiate, with two petals in the upper lip and three in the

lower—sometimes the upper lip shows no trace of its origin from two petals; the stamens are epipetalous and alternate with the sepals; the posterior stamen is generally aborted, rarely represented by a staminode, and the four are generally didynamous (Fig. 189, I), rarely equal (*Mentha*); the pistil is bicarpellary, but becomes four-lobed and four-celled as in the *Boraginaceæ*; the style is gynobasic and the fruit consists of four dry one-seeded nutlets.

The following are the more important British *Labiatæ*:—

The **dead-nettle** (*Lamium*), of which common forms are *L. album*, with white flowers (Fig. 189, I, II), *L. purpureum*, with reddish flowers, *L. Galeobdolon* (the **yellow archangel**), with yellow flowers, and *L. amplexicaule* (the **henbit**).

The **wood sage** (*Teucrium Scorodonia*). The upper lip of the corolla is very short, with two small teeth, between which the stamens protrude. The pale yellow flowers arise in pairs, and form one-sided racemes.

The **bugle** (*Ajuga*), of which the **creeping bugle** (*A. reptans*) is the commonest species, has blue flowers in leafy spikes. The upper lip of the corolla is very short, erect, and tooth-like.

Stachys includes several British species. The **hedge stachys** (*S. sylvatica*) is a very common, rough, hairy herb, with a peculiar smell, and purple flowers in long terminal spikes. The **betony** (*S. Betonica*) is also very common; the leaves are coarsely crenate. *S. palustris* is the **marsh stachys** found growing in ditches, and *S. arvensis*, the **field stachys**, is a low, spreading annual, with smaller flowers, found growing in fields and waste places.

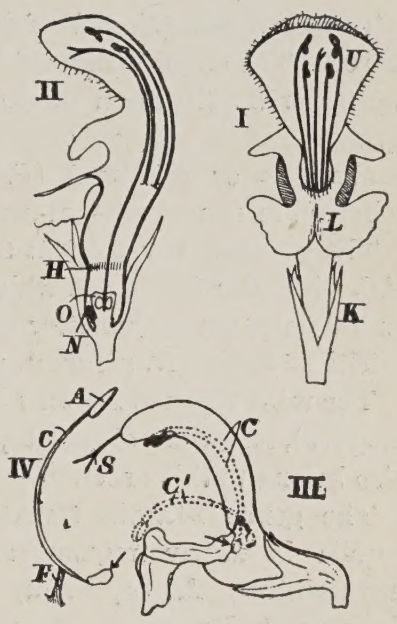


FIG. 189. *Labiatæ*. I. Flower of the Dead-nettle (*Lamium*), from the front. K=calyx; L=lower lip; U=upper lip of the corolla representing two petals. The didynamous stamens and bifid stigma are covered by the upper hood-like lip of the corolla. II. The same in vertical section from the side. H=ring of hairs; N=nectary; O=ovary. Note the divergent anther-lobes. III. Flower of the Sage (*Salvia*), from the side. C=the connectives of the two stamens supposed to be visible through the corolla; C′=the connectives of the stamens in the depressed condition brought about by insect visitation; S=stigma. The arrow is directed towards the sterile anther-lobes. IV. A single stamen of the same. A=fertile anther-lobe; C=elongated connective; F=filament. The arrow points to the sterile lobe.

Galeopsis includes the **hemp nettle** (*G. Tetrahit*), a coarse annual covered with long stiff hairs; the anthers open by transverse slits bordered with hairs.

The **black horehound** (*Ballota nigra*) is a coarse hairy perennial, with a strong odour.

The **skullcap** (*Scutellaria*) has solitary flowers in the axils of the leaves. The calyx is divided into two entire lips, and after flowering the upper lip closes on the lower one; the corolla has nearly closed lips.

Prunella or **self-heal** (*P. vulgaris*) has whorled purple flowers collected in dense terminal heads.

The **ground ivy** (*Nepeta Glechoma*) is a common creeping perennial, with blue flowers, in which the posterior (inner) stamens are the longer ones, not the anterior ones, as is usually the case.

The **catmint** (*N. cataria*), with an erect stem, is also common.

The **wild thyme** (*Thymus Serpyllum*), **wild marjoram** (*Origanum vulgare*), and the **calamints, basil,** and **basil thyme** (*Calamintha*) also belong to this order.

The genus *Mentha* (**mint**) includes several wild species. The corolla is nearly regular, and four-lobed. *M. sylvestris* is the **horse-mint**; *M. aquatica*, the **water-mint**; *M. arvensis*, the **corn-mint**, &c.

The **gipsywort** (*Lycopus*) has two stamens only.

The **wild sage** (*Salvia Verbenaca*), and the cultivated exotic forms, have only two stamens, and these are modified in order to assist cross-pollination by insects (see p. 314, and Fig. 189, III, IV).

Commonly cultivated exotic forms are the **lavender** (*Lavandula*), **sweet marjoram** (*Origanum*), **balm** (*Melissa*), **sweet basil** (*Ocymum*), **rosemary** (*Rosmarinus*), &c.

The order is generally easily recognized by the square stems with opposite leaves, bilabiate flowers, didynamous stamens, and characteristic ovary and fruit. The latter character distinguishes the order from those *Scrophulariaceæ* which have a somewhat similar corolla; from the *Boraginaceæ* they may be distinguished by the opposite leaves, and reduction in the number of stamens.

The floral formula is generally K (5), [C (5), A 4], $G\underline{(2)}$. (See floral diagram, Fig. 160, p. 297.)

(*b.*) OVARY INFERIOR.

Order 29. **Campanulaceæ** (Fig. 190). A large order represented in Britain by four genera only. The plants are generally herbs with simple exstipulate alternate leaves, and flowers in racemes, spikes, or heads, or solitary. The flowers are generally pentamerous with a tricarpellary gynæcium; sometimes there are five carpels, so that the flowers are actinomorphic, or there may be only two; the calyx is sometimes provided with a stipular epicalyx; the corolla is often regular and bell-shaped (**campanulate**), sometimes bilabiate and irregular (*Lobelia*, &c.); stamens five in number, and free from the corolla, rarely epipetalous (*Lobelia*); anthers free, rarely syngenesious (*Lobelia*); style simple, with two to five stigmas; fruit, a capsule, often opening by valves or pores below the persistent calyx.

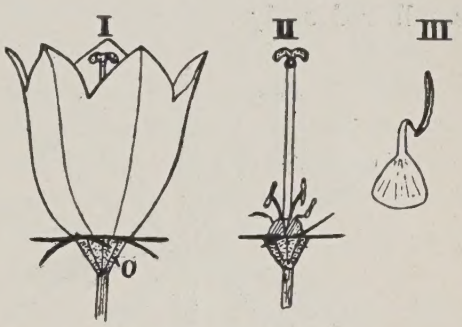


FIG. 190. *Campanulaceæ*. I. Flower of *Campanula*. O=the inferior ovary. II. Flower of the same from which the corolla has been removed. The flower is markedly protandrous—the stigmas are in a receptive condition when the stamens have dehisced and withered. III. A single stamen of the same, showing the broad basal part of the filament. These basal portions serve to guard the nectary, which is situated at the base of the style.

The genus **Campanula** (Fig. 190) includes many British species with a campanulate corolla, and either three or, rarely, five carpels. Many exotic forms are cultivated. *C. Rapunculus* is the **rampion**, which was formerly much cultivated for the sake of its tuberous roots.

The **sheep's-bit** (*Jasione*) is a little plant much resembling a scabious, or one of the *Compositæ*. The blue flowers are in terminal heads, but the stamens are monadelphous, and the bilocular ovary contains many ovules.

Phyteuma bears also heads of flowers.

The genus *Lobelia* is often separated as a distinct order on account of the irregular flowers with epipetalous stamens and syngenesious anthers. During the development of the flower the pedicel undergoes twisting through 180°, so that parts of the flower which were originally anterior become posterior, and vice versa.

The order may generally be recognized by the five stamens free from the corolla, the longitudinal dehiscence of the anthers, and

inferior ovary with many ovules. The fruit is a capsule. The freedom of the stamens from the corolla is a character which is only shared among British Gamopetalæ by the *Ericaceæ*. The plants generally have a milky latex contained in laticiferous vessels (as also in many *Compositæ*, *Papaveraceæ*, &c., see p. 450).

Floral formula, K (5), C (5), A 5, G $\overline{(2—5)}$.

* Order 30. **Rubiaceæ.** The madder family (Fig. 191). A very large family, including over 4,000 species of herbs, shrubs, and trees, some of which are among the commonest of weeds both in tropical and temperate climates. The leaves are simple, opposite, and stipulate, the stipules being sometimes large and leafy, at others small and scaly.

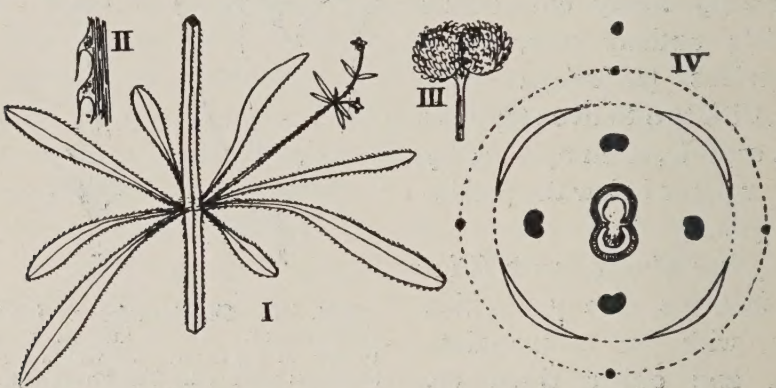


FIG. 191. *Rubiaceæ*. I. *Galium Aparine* (Cleavers). Six of the eight leaves shown are regarded as stipules. The edges and midribs of the leaves, as well as the angles of the stem, are provided with sharp recurved prickles by means of which the plant scrambles over bushes. II. A portion of the edge of a leaf of the same, showing the recurved prickles. III. Fruit of the same, a small burr covered with hooked hairs and easily distributed by animals. IV. Floral diagram of the same.

All the British forms belong to the **Stellatæ**, one of the three tribes into which the order is divided, characterized by the possession of large stipules similar to the leaves (Fig. 191, I), and a bilocular ovary with one ovule in each cell.

The genus *Galium* includes the **crosswort, ladies'-bedstraw, cleavers,** &c. (Fig. 191). The leaves appear to be in whorls of four to eight, but all except two in each whorl are regarded as stipules, and they possess no buds in their axils. The flowers are tetramerous, but with two carpels, each of which forms a small one-seeded achene-like fruit, often covered with small hooked hairs (Fig. 191, III).

The **woodruff** (*Asperula*) has flowers with longer corolla-tubes than in *Galium*.

The **madder** (*Rubia*) has a five-lobed corolla and a baccate fruit.

The **field madder** (*Sherardia*), with pink or lilac flowers in heads, belongs to the last of the British genera.

Exotic forms include **coffee** (*Coffea arabica*, &c.), with two seeds enclosed in a berry; *Cinchona*, from which Peruvian bark and quinine are obtained; the rhizome of *Rubia tinctorum* yields the dye madder; the rhizome of *Cephaelis* yields ipecacuanha; *Bouvardia*, *Gardenia*, &c., are cultivated for their flowers, &c.

The British forms are easily recognized by the apparent whorls of leaves, and small tetramerous or pentamerous flowers.

Floral formula, K (4–5 or 0), [C (4–5), A 4–5], $G\overline{(2)}$.

Order 32. **Caprifoliaceæ.** The honeysuckle tribe. Generally shrubs or small trees, sometimes herbs; with simple or compound, exstipulate, opposite leaves, and pentamerous, regular or irregular (zygomorphic) flowers. Inflorescence various, generally heads (**honeysuckle**), spikes (**snowberry**), or corymbose cymes (*Viburnum* and **elder**); carpels usually three in number, but varying from one to five, forming a multilocular ovary with one or more ovules in each cell; fruit generally a berry or a drupe.

The genus *Viburnum* includes shrubs and small trees with entire or palmately lobed, simple leaves, a rotate five-lobed corolla, and, generally, three stigmas. The ovary at an early stage is trilocular, but two carpels early become aborted; fruit a one-seeded berry. The **wayfaring-tree** (*V. Lantana*) has undivided leaves, and flowers which are all perfect; the **wild guelder rose** (*V. Opulus*) has the outer florets of the inflorescence enlarged and neuter, serving merely for the attraction of insects; the cultivated form of **guelder rose** has all its florets neuter; *V. Tinus*, from southern Europe, is the **laurustinus.**

The **elder** (*Sambucus*) has also regular flowers, but the leaves are pinnately compound. There is a three to five-lobed stigma, and the fruit is an inferior, berry-like drupe, containing a small number of seeds, each surrounded by an endocarp.

The **moschatel** (*Adoxa*) is a low herb, very different in general appearance to the other members of the order. It is found in damp woods, and has ternate leaves and small greenish flowers, five of which form a small terminal head. Of the five flowers, the terminal one has four petals and eight stamens, and the lateral ones five petals and ten stamens. The increase in the number of stamens in this genus is due to the division of each of the four or five rudiments

during development. The apparent calyx, which is composed of two or three sepals, is sometimes regarded as an involucre.

The **honeysuckle** (*Lonicera*) belongs to the division of the order with irregular (zygomorphic) flowers. The flowers are in heads; the corolla is two-lipped, with four petals in the upper one, and one in the lower (Fig. 228, IV, p. 485); the style is simple, with a capitate stigma; the ovary is bi- or trilocular, with several ovules in each cell; fruit a berry, with few seeds, because only a few of the ovules mature. In *L. Xylosteum* the flowers are in pairs, and are united by their ovaries.

Several exotic genera are cultivated, including the **snowberry** (*Symphoricarpus*) with white berries; *Weigelia* is an ornamental shrub with a large nectary at the bottom of the corolla, and a bilocular capsular fruit; *Leycesteria*, with a pentalocular ovary, &c.

This order is not a very natural one, but may generally be recognized by the opposite exstipulate leaves, pentamerous flowers with epipetalous stamens, and multilocular inferior ovary, except in *Viburnum*, which is multilocular only at an early stage.

Floral formula, K (5), [C (5), A 5], $G\overline{(2-5)}$.

* Order 32. **Valerianaceæ.** The valerian family. A family related to some of the *Caprifoliaceæ* (*Viburnum*) and to the following order (*Compositæ*). It is represented in Britain by three genera, including the **red valerian** (*Centranthus*), **common valerian** (*Valeriana*), and **corn salad** (*Valerianella*).

The leaves are opposite and exstipulate, simple or compound; flowers zygomorphic and pentamerous, but with reduction of the stamens generally to three, and of the carpels also to three, only one of which develops (as in *Viburnum*); calyx rudimentary, often forming after flowering a pappus of ten rays; fruit unilocular with a single suspended seed.

The **red valerian** (*Centranthus*) has a spurred corolla, and only one lateral stamen. The limb of the calyx is represented by a flattened rim, which unrolls later into a plumose pappus.

The genus *Valeriana* includes three British species. Calyx and pappus as in *Centranthus*; corolla slightly saccate or pouched, but not spurred; stamens three. The **marsh valerian** (*V. dioica*) has rose-coloured unisexual flowers in terminal corymbose cymes.

Corn salad (*Valerianella*) has small white or pale blue flowers with a saccate corolla; no pappus.

The order is distinguished among Gamopetalæ with an inferior

ovary, by the inconspicuous calyx, spurred or saccate corolla, and reduction in the stamens and carpels. Ovary and fruit, one-seeded.

Floral formula (generally), K 0, [C (5), A 3], $G\overline{(3)}$.

** Order 33. **Compositæ.** This, the largest natural order of Phanerogams, includes more than 10,000 species, distributed in nearly 800 genera, of which about forty have British representatives, and many others are cultivated. They are represented over nearly the whole of the earth's surface, but are especially abundant in temperate and sub-tropical regions, where some species are shrubby or even arborescent.

The British forms are herbs with simple or compound, alternate or sometimes opposite, exstipulate leaves. The flowers are always arranged in capitula, which are surrounded by an involucre of bracts. The common receptacle may or may not bear scales or **paleæ** between the flowers. The flowers, or florets, make up an inflorescence which opens from without inwards, and each flower is generally protandrous, the anthers maturing before the stigmas. Different kinds of flowers, hermaphrodite, male, female or sterile, are commonly present in the same head; when this is the case the outer florets (ray florets) are female or neuter, and the inner ones (disc florets) are hermaphrodite or male. The ray florets differ in form, and often in colour, from those of the disc, being modified for attractive purposes, and so serve physiologically as a corolla to the whole inflorescence.

Calyx rudimentary, often represented by a ring of simple or branched hairs constituting a pappus; corolla, tubular and five-lobed, or irregular and expanded on one side so as to become ligulate, with either three or five teeth at the margin of the limb, sometimes bilabiate; stamens epipetalous, with short filaments and long coherent anthers (syngenesious) forming a tube enclosing the style (Fig. 154, III, p. 290); gynæcium bicarpellary, with a unilocular ovary, containing a single basal anatropous ovule; stigma bifid; fruit practically an achene, but differing from the typical form (as found in some *Ranunculaceæ* and *Rosaceæ*) in being inferior and syncarpous.

It is convenient to divide this large order into three sub-orders, according as (1) all or some of the florets are tubular (e. g. regular and five-toothed); (2) all the florets are ligulate, or (3) the corollas of the flowers are bilabiate.

(i) **Tubulifloræ.** All the florets tubular, and hermaphrodite; or those of the disc tubular, while the florets of the ray form one or two rows of ligulate female or sterile flowers.

This division includes most of the British representatives of the order, among which are the following:—

The **hemp agrimony** (*Eupatorium*), with opposite leaves and florets all tubular; **golden rod** (*Solidago*); **daisy** (*Bellis*), without a pappus; **chamomile** (*Anthemis*), also destitute of a pappus; **milfoil** or **yarrow**, and **sneezewort** (*Achillea*); **tansy** (*Tanacetum*); **coltsfoot** and **butter-bur** (*Tussilago*); **groundsel, ragwort**, &c. (*Senecio*); **burdock** (*Arctium*); **thistle** (*Carduus*), with prickly leaves and bristles between the florets; **cornflower** and **knapweeds** (*Centaurea*); **hawkbit** (*Leontodon*), &c.

Commonly cultivated forms include *Aster*; the '**China aster**' (*Callistephus hortensis*); *Doronicum*; **sunflower** (*Helianthus annuus*); **Jerusalem artichoke** (*H. tuberosus*); *Zinnia*; *Rudbeckia*; *Dahlia*; **marigold** (*Calendula*), &c.

(ii) **Labiatifloræ.** A small group of South American forms, some or all of the florets of which have bilabiate corollas.

(iii) **Liguliflorae.** All the florets ligulate and hermaphrodite. Most of the forms contain a milky latex contained in laticiferous vessels.

To this sub-order belong the following British plants: **dandelion** (*Taraxacum*); **sowthistle** (*Sonchus*); **hawkweed** (*Hieracium*); **chicory** (*Cichorium*); **nipplewort** (*Lapsana*), &c.

The order is recognized by the arrangement of flowers in capitula, by the epipetalous syngenesious anthers (by which it is distinguished from *Dipsaceæ*), and by the one-seeded inferior fruit. Ligulate florets, when present, are distinctive, as they are unknown in any other family.

Floral formula, K pappus, 0 or (5), [C (5), A 5], $G\underline{(2)}$.

II. Sub-Class Incompletæ.

Order 34. **Urticaceæ.** The nettle family. A large order, including trees, shrubs, and herbs, and represented in the British flora by four genera only; the **stinging-nettles** (*Urtica*), **pellitory** (*Parietaria*), **hop** (*Humulus*), and **elm** (*Ulmus*).

Leaves opposite or alternate, often stipulate; flowers small and usually unisexual, with a simple sepaloid perianth with four or five segments; stamens opposite the segments of the perianth in consequence of the spiral arrangement of the floral organs; ovary superior, generally unilocular but sometimes bilocular, with one, sometimes two, ovules.

The family is divided into a number of sub-orders (all of which are often raised to ordinal rank), as follows:—

(i) **Urticeæ.** Generally herbs. Flowers unisexual; filaments inflexed in the bud; ovary one-celled. The genus *Urtica* includes the **stinging-nettles**, of which there are two British species. They have opposite leaves, and stinging hairs distributed over their entire surfaces. The **small nettle** (*U. urens*) is monœcious, and has its flowers in axillary clusters; the **great nettle** (*U. dioica*) is generally dicœcious, and bears flowers in long axillary spikes.

The **wall pellitory** (*Parietaria*) has alternate leaves devoid of stinging hairs.

(ii) **Cannabineæ.** Herbs with stipulate opposite leaves, and dicœcious flowers. Filaments straight in the bud; ovary one-celled, with one ovule; stigmas two.

The **hop** (*Humulus*) is a twining plant and occurs both cultivated and wild. The male flowers have a perianth of five parts; the female flowers are borne in spikes somewhat resembling fir-cones. The bracts and fruits are covered with yellow glands containing a bitter principle, to which the useful properties of hops are due.

The **hemp** (*Cannabis sativa*) also belongs to this sub-order. Its seeds are used for birds' food, and its tough bast-fibres for ropes, &c.

(iii) **Ulmeæ.** The elms are trees with distichous, alternate, oblique leaves, and caducous stipules. Flowers hermaphrodite, borne in glomerules in the axils of the leaves of the previous year; ovary one- or two-celled, each containing a single ovule; fruit, a samara, one-seeded (Fig. 167, IV, p. 319).

(iv) **Moreæ.** A purely exotic tribe, consisting of trees with alternate leaves and milky latex, and including the **mulberry** (*Morus*) and **fig-tree** (*Ficus*), with the **india-rubber plant** (*F. elastica*), the **banyan** (*F. indica*), &c.

The order is distinguished by the unisexual, small green flowers (except *Ulmeæ*); stamens opposite the divisions of the perianth; and one-seeded fruit.

Floral formula (generally), P (4), A 4, $G\underline{1}$.

Order 35. **Cupuliferæ.** (Fig. 192, and Fig. 165, p. 304.) The plants in this order are trees or shrubs, with alternate stipulate leaves, and monœcious flowers generally arranged in catkins (see Fig. 165, p. 304). Perianth of five (sometimes four or six) segments, or absent; stamens opposite the perianth leaves (as in the *Urticaceæ*); ovary superior or inferior; fruit one-seeded. The female flowers are often surrounded

by an investment of bracts which, later, form the cupule of the fruit (Fig. 192, V, VI).

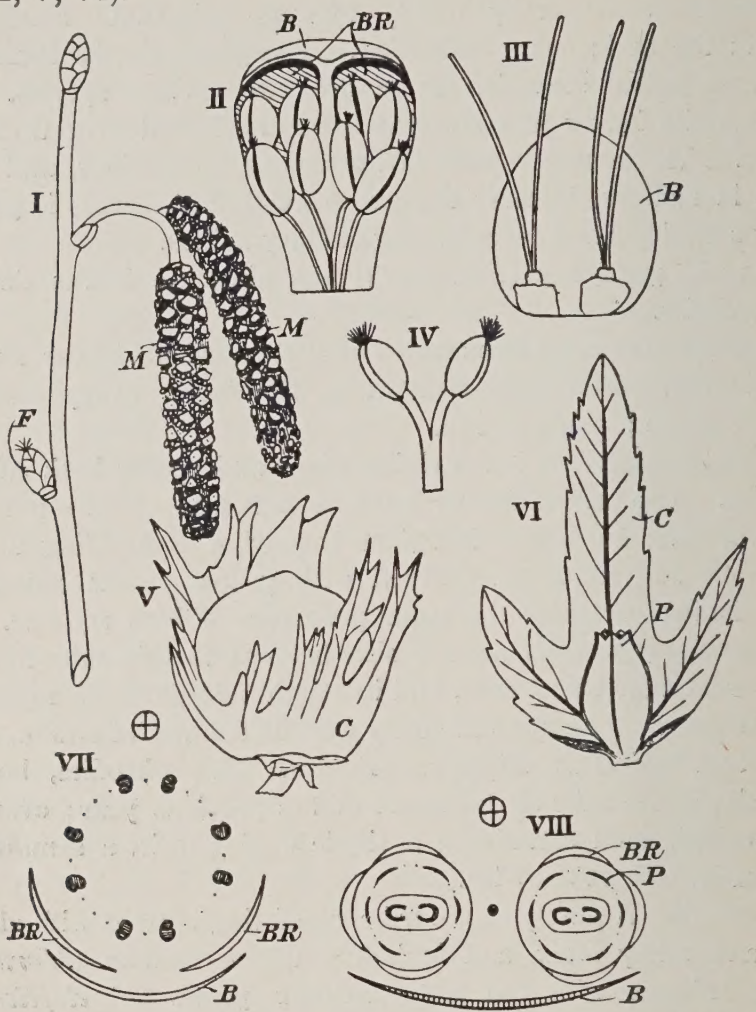


FIG. 192. *Cupuliferæ* (see also Fig. 165, p 304). I. Branch of Hazel (*Corylus*). F=bud-like female catkin with red stigmas projecting at the top; M, M = pendulous male catkins. II. One scale from a male catkin of the same. B=the scale or bract enclosing two bracteoles BR, and a flower consisting of four forked stamens. III. One of the fertile scales (or bracts) from a female catkin of the same. B=the scale or bract enclosing two female flowers each with a rudimentary epigynous perianth and three bracteoles (see VIII). IV. One of the forked stamens of the Hornbeam (*Carpinus*). V. Fruit (nut) of the Hazel, showing the leafy cupule (C) formed by the growth of the three bracteoles. VI. Fruit of the Hornbeam (*Carpinus*). C=the three-lobed cupule; P=the rudimentary persistent perianth. VII. Diagram showing a single male flower of the Hazel with its bract B and bracteoles BR, BR (cp. II). VIII. Diagram showing the two female flowers enclosed within a scale of the female catkin of the Hazel (cp. III and Fig. 165). The middle flower is aborted. B=bract or scale; BR=one of the three bracteoles surrounding a single flower; P=rudimentary perianth.

The order is conveniently divided into the following sub-orders, all of which are sometimes raised to ordinal rank;—

(i) **Betuleæ.** Includes the **birch** (*Betula*) and **alder** (*Alnus*). The male catkins of the birch are pendulous, and each bears a number of bracts. Within each bract there are two bracteoles and an inflorescence of three male flowers, each with two forked stamens. The female catkins of the birch are at first erect, and also bear a number of bracts. Each bract encloses two bracteoles and three female flowers, each of which consists of a bilocular ovary and two styles.

In the male catkin of the alder the bracts are also three-flowered, but each flower has a small four-lobed perianth and four stamens. There are four bracteoles. The female inflorescence resembles that of the birch in essential structure excepting that there are four bracteoles and only two flowers, the middle one of the dichasial cyme being suppressed (see p. 305).

(ii) **Quercineæ.** Fruit enclosed in a cup-shaped involucre or cupule.

The **oak** (*Quercus*) has pendulous male catkins, with single flowers in the axils of the bracts. The perianth has from four to seven (generally five) lobes, and the stamens vary in number from six to twelve. The female flowers occur singly or in small groups ; each flower arises in the axil of a bract, and has a perianth and an inferior ovary with three cells and three styles. Each female flower is surrounded by an involucre of small bracts, which becomes the cupule. Fruit a nut, one-seeded by abortion.

The **beech** (*Fagus*) has globular male catkins with stalked flowers, each with a campanulate perianth, and from eight to twelve stamens. The female flowers are arranged in pairs within a bristly cupule. There are four filiform bracteoles. Each female flower consists of a superior perianth and a three-celled inferior ovary with three styles. Fruit a nut, enclosed in pairs in the hard involucre, which splits into four valves.

In the **edible chestnut** (*Castanea*) the catkins are very long, and may contain both male and female flowers. In the axil of each bract there are seven male flowers or three female ones. The three female flowers are enclosed in one cupule.

(iii) **Corylaceæ.** Fruits enclosed in a leafy cupule. The **hornbeam** (*Carpinus*) has its flowers in pendulous catkins. The male catkin consists of bracts, each bearing four to ten forked stamens (Fig. 192, IV) ; there is no perianth. In the female catkin the flowers are arranged in pairs ; each flower has a perianth, and is accompanied by three bracteoles ; ovary inferior and bilocular with two ovules in

one cell and none in the other; fruit a nut, with a three-lobed cupule, formed by the growth and cohesion of the bracteoles (Fig. 192, VI).

The **hazel** (*Corylus*) has pendulous male catkins (Fig. 192, I, M), with scales (bracts), each enclosing two bracteoles, and a male flower consisting of four forked stamens (Fig. 192, II, VII). The female catkins are bud-like structures (Fig. 192, I, F), each consisting of a number of bracts with the red stigmas projecting at the top. Two flowers arise together within each of the upper bracts (the lower bracts of the catkin are sterile); ovary as in *Carpinus*; fruit a nut enclosed in the enlarged leafy bracteoles (Fig. 192, V).

Order 36. **Salicaceæ.** The willow family (Fig. 151, III, IV, p. 282). An order containing two genera only, *Salix* (the **willows**) and *Populus* (the **poplars**).

Trees or shrubs with alternate stipulate leaves and diœcious flowers arranged in hairy catkins. Each scale (bract) of the catkins encloses a single flower; perianth absent in both male and female flowers; male flowers of one or more stamens; female flowers of two carpels, forming a unilocular ovary containing many ovules on parietal placentæ; fruit, a capsule; seeds with a tuft of silky hairs at the base.

The **willow** (*Salix*) has entire bracts, and male flowers, with (usually) two stamens only.

The **poplar** (*Populus*) has a cup-shaped nectary (sometimes called a perianth) under each flower; the bracts are lobed or toothed, and the male flowers have from four to thirty stamens.

The order is distinguished from the *Cupuliferæ* by the absence of a cupule, the diœcious flowers, and the structure of the ovary and fruit. The *Cupuliferæ* and *Salicaceæ* may be included in one order, the **Amentaceæ** or catkin family.

Order 37. **Euphorbiaceæ.** The spurge family (Fig. 193). The proper systematic position of this order is uncertain; some writers place it in the *Incompletæ*, and others (as petals are present in many exotic genera) with the *Dichlamydeæ*.

The family is a very large one, including some 3,500 species, and is especially abundant in the tropics.

The plants are herbs, shrubs, or trees, and generally possess latex, which may be milky (e. g. *Euphorbia*) or clear (*Mercurialis*). Leaves stipulate or exstipulate; flowers unisexual, monœcious or diœcious; perianth, three- to five-lobed or absent, sometimes, in exotic forms, in two whorls; stamens from one to eight, sometimes repeatedly branched (e. g. *Ricinus*); ovary usually trilocular with one or two

ovules in each cell; fruit usually dry and dehiscent, splitting septicidally into three cocci.

The British genera belonging to this order are *Euphorbia*, *Mercurialis* and *Buxus*, representing three of the sub-orders into which the family is divided.

The **spurges** (*Euphorbia*) are herbs (in the British species) with abundance of milky latex, contained in laticiferous cœnocytes (p. 451). Leaves alternate in the lower part of the stem, but opposite in connexion with the inflorescences.

Each inflorescence (Fig. 193) consists of a monœcious head (**cyathium**) containing a number of male flowers, each of which consists of a single stamen, with a scale-like bract at its base, and a single female one formed of a trilocular ovary and branching stigmas, the whole enclosed in a tubular involucre with four or five lobes. Between the lobes of the involucre semilunar glands are developed. The proof that the cyathium is an inflorescence and not a single flower is found by comparison with some exotic forms in which an involucre is developed around each stamen. The inflorescences themselves are arranged in cymose umbels. Some exotic species of *Euphorbia* are shrubs; many African forms closely simulate *Cactaceæ* in appearance, having thick succulent stems and small deciduous leaves.

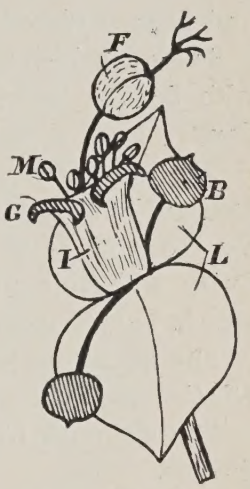


FIG. 193. Cyathium of a Spurge (*Euphorbia*). B = bud; F = female flower; G = glands; I = tubular involucre; L = leaves; M = one of the male flowers consisting of a single stamen.

Dog's mercury (*Mercurialis*) is a small herb with opposite leaves and small green flowers on axillary peduncles. Dicœcious; perianth of three valvate segments; ovary two-celled and two-lobed with diverging styles.

The **box** (*Buxus*) is a shrub with opposite evergreen leaves, and monœcious flowers formed in axillary clusters, each containing several male and one or two female flowers. The male flowers have a perianth of four segments with four stamens opposite to them; the female flowers also have a perianth, and a three-celled ovary.

Order 38. **Chenopodiaceæ.** The goosefoot family. A widely-spread order, occurring especially near the sea. Represented in Britain by six genera, *Chenopodium*, *Atriplex*, *Beta*, *Salicornia*, *Suæda*, and *Salsola*.

The plants are generally herbs, with alternate, sometimes opposite, exstipulate leaves; flowers usually hermaphrodite, but sometimes unisexual, and with a sepaloid perianth of, generally, four or five segments; the stamens lie opposite the perianth-segments; the superior ovary is one-celled and one-ovuled with two or three styles; fruit achenial, consisting of a single seed contained in a thin pericarp enclosed in the persistent perianth.

The **goosefoot** (*Chenopodium*), includes several British species, which have small hermaphrodite flowers collected in little clusters, and often covered with mealy dust.

Several British species are included in the genus *Atriplex* (**orache**), with flowers like those of *Chenopodium* but unisexual; the female flowers have a perianth of two segments only.

The **beet** (*Beta*) includes a wild form (*B. maritima*) as well as the **mangold** or **mangel wurzel**, the **red beet**, and the **white beet** grown for the sake of its sugar. The flowers are hermaphrodite, and the ovary and fruit are enclosed in the succulent base of the perianth, which, later, becomes enlarged and hard.

The **saltwort** (*Salsola*), **sea-blite** (*Suæda*), and **marsh samphire** (*Salicornia*), are sea-shore plants with succulent stems.

The **spinach** (*Spinacia*) belongs to an exotic genus with diœcious flowers.

The order is distinguished by the exstipulate leaves; small green flowers in dense inflorescences; stamens opposite to the perianth segment; and one-celled ovary with one ovule.

Floral formula, P (5 or less), A 5 or less, G $\underline{(3-2)}$.

Order 39. **Polygonaceæ.** The knot-grass family (Fig. 194). This order contains about 600 species, spread over every part of the globe. Only three genera (*Polygonum*, *Rumex*, and *Oxyria*) are indigenous to Britain.

The plants are generally herbs with simple alternate leaves and scarious stipules. The stipules form a ring round the stem inside the petiole (Fig. 194, I, s). Flowers small, clustered in the axils of the leaves, or forming racemes or spikes.

The perianth is generally trimerous and in two whorls, but the segments are all alike (some authorities regard the outer whorl as a calyx and the inner as a corolla, and classify the order with the *Dichlamydeæ*); stamens also usually in two whorls but variable in number (five to eight), perigynous or hypogynous; ovary superior and unilocular, but generally consisting of two or three carpels as

shown by the free stigmas and styles; ovule solitary and basal; fruit dry and indehiscent (a nut), enclosed by some or all of the leaves of the persistent perianth.

The genus *Polygonum* includes the **knotgrass, persicaria, water-pepper,** &c. The flowers are green or red, and the perianth generally has five segments. The ovary is triangular in shape.

The genus *Rumex* includes the **docks** and **sorrels,** of which there are several British species. They have a six-cleft perianth in two whorls, six stamens, and three carpels (Fig. 194, VI). The three inner

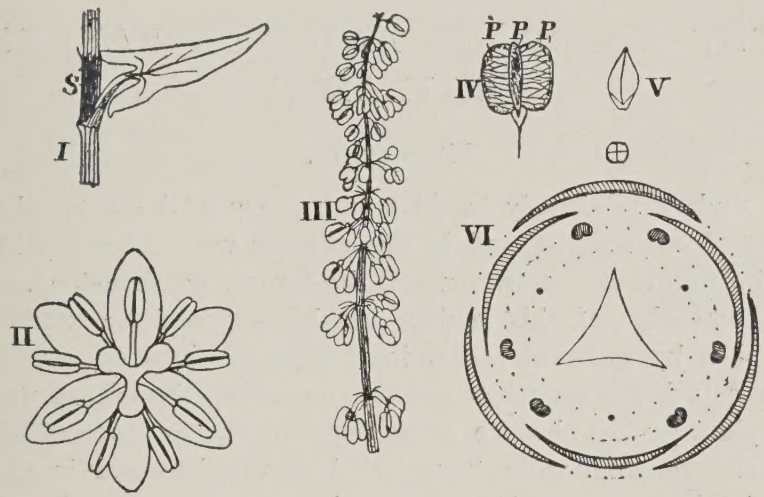


FIG. 194. *Polygonaceæ.* I. Sorrel (*Rumex*). Showing the sagittate leaf and the stipules (S) forming a sheath round the stem within the leaf-stalks. II. Flower of Rhubarb (*Rheum*) seen from above. The perianth is in two trimerous whorls; stamens nine in number, six in an outer and three in an inner whorl; carpels three indicated by the three stigmas. III. A collection of fruits of the Sorrel. IV. A single fruit of the same, showing the enlarged persistent perianth leaves (P, P, P). V. The triangular nut from IV. VI. Floral diagram of *Rumex*.

perianth leaves persist and enlarge, and enclose the triangular fruit (Fig. 194, IV, V). The sorrels have, usually, dicœcious flowers. Their leaves contain oxalic acid.

The **mountain sorrel** (*Oxyria*) has four perianth leaves and two carpels and stigmas.

Important exotic forms are **rhubarb** (*Rheum*, Fig. 194, II) and **buckwheat** (*Fagopyrum esculentum*).

The order is easily distinguished by the ochreate stipules and (generally) triangular ovary and fruit.

Typical floral formula, P 3+3, A 3+3, G$\underline{(3)}$.

PART III

THE PHYSIOLOGY OF PLANTS

CHAPTER XXIII

THE NUTRITION AND RESPIRATION OF PLANTS

NUTRITION.

THE student is already familiar with many of the facts relating to this part of our subject, and in this chapter we shall study in more detail the nature of respiration and the sources of plant-food. Much of our knowledge of this subject has been gained by experimental culture, i. e. by growing plants in watery solutions of various substances, called **Water Culture**, and observing the effects produced on the plant by the absence or presence of one or more of the substances experimented with. Thus the plants may be grown in a solution from which iron or potassium or any other special element is excluded, and the effects produced (if any) determined by comparison with other plants of the same kind, grown in a solution of the same nature, but to which the special element (iron, potassium, &c.) has been added in the form of a soluble salt.

Make a solution of the following soluble chemical salts:—

Potassium nitrate (KNO_3)	1·0 gram.
Sodium chloride ($NaCl$)	0·5 „
Calcium sulphate ($CaSO_4$)	0·5 „
Magnesium sulphate ($MgSO_4$)	0·5 „
Calcium phosphate ($Ca_3(PO_4)_2$)	0·5 „
Ferric chloride solution (Fe_2Cl_6)	A few drops.
Water	1000 cc.

The salts used must be chemically pure, as a very small quantity of impurity will vitiate all the results. Large wide-mouthed bottles, or glass cylinders, may be used to contain the solution, and each must be provided with a cork; the bottles used must be made

scrupulously clean, and the solution itself should be boiled for some time before it is placed in the receptacles. It is also advisable to make black paper covers for the bottles or cylinders, in order to keep out as much light as possible from the water and roots, as light favours the growth of minute organisms in the water and interferes somewhat with the nutrition of the plants. Two fairly large holes are bored through the cork, and in one of these a short wide glass tube is fitted to admit air, while in the other hole the young plant to be experimented with is fixed by means of cotton wool or soft asbestos (Fig. 195). Young plantlets of the wallflower or barley are suitable for the experiments, but even with the greatest care, some of the specimens die, owing to various causes, the commonest of which is 'damping off' from the attack of *Pythium* and other fungi.

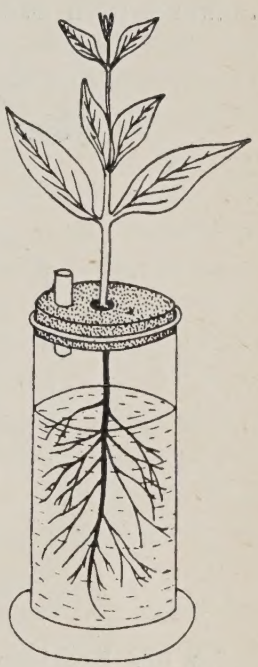


FIG. 195. Water-culture experiment.

In such a solution as the above, which contains the elements potassium, sodium, calcium, magnesium, iron, phosphorus, sulphur, chlorine, nitrogen, and oxygen, an ordinary green aërial plant will live and go through its normal development, even up to the formation of flowers and fruit. Of the chemical elements present in protoplasm (C . H . O . N . S . P .) it will be noticed that two, carbon and hydrogen, are not present in the salts named, and must therefore be obtained by the plant from other sources: the former is obtained from the carbon-dioxide of the air with which the aërial part of the plant is surrounded, and the latter from the water (H_2O) in which the salts are dissolved.

Floating green water-plants such as the duck-weed (*Lemna*) may also be used for these experiments, but submerged water-plants are not suitable, because the necessary carbon is in such cases normally obtained from carbon-dioxide dissolved in the water, and our experimental solution, which has been boiled, should contain none. In the preparation of the experimental solution described above, only **inorganic** substances are employed, nor are organic substances present in the atmosphere in a form capable of being used by plants, yet **organic** substances, both non-nitrogenous, such as starch, and nitrogenous, such as proteids, are abundantly formed in the leaves, as will

be shown later. It is clear, therefore, that a green plant possesses the remarkable power of manufacturing organic substances (e.g. starch) from inorganic constituents (e.g. carbon-dioxide and water), and this is an operation of the greatest physiological importance. Plants which are not green, i.e. do not contain chlorophyll, such as fungi, the dodder, &c., are unable to do this, and are dependent on *complex* carbon compounds for their carbonaceous food; such plants must be either **saprophytes**, which obtain their carbon from dead and decaying organic matter, e.g. mushroom, or **parasites** such as *Pythium*, which obtain it from living organisms. If fungi are to be grown in culture-

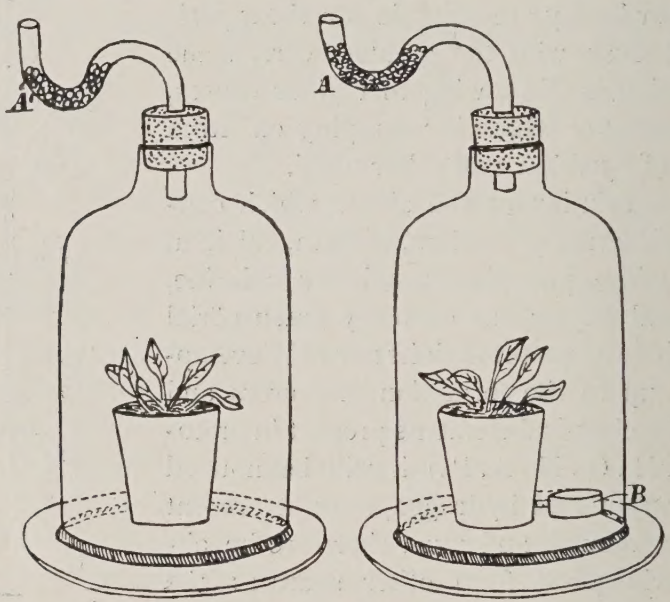


FIG. 196. Experiment to show that an ordinary green plant depends on the carbon-dioxide in the air for its carbon. A=tube containing soda-lime, which removes the CO_2 from the entering air; A'=tube containing fragments of pumice, which has no action on the entering air; B=vessel containing caustic potash solution to absorb the CO_2, which is at first present in the air of the bell-jar.

solutions it is clear that the one above described will not suffice, as it contains no carbonaceous food, and this must be added in the form of sugar or some other complex carbon-compound.

That an ordinary green plant depends for its carbon on the carbon-dioxide in the air may be demonstrated by experiment (Fig. 196). Two bell-jars are taken, and each is fitted with a perforated india-rubber stopper and a bent glass tube as shown in the illustration; one of the tubes (A) is partly filled with soda-lime, while the other (A') contains only dry sawdust or fragments of pumice. Two similar plants or cuttings should be prepared for the experiment by keeping

them in the dark for a couple of days or more, until all the starch has disappeared from the leaves. This is ascertained by plucking one of the leaves, boiling it in water for about a minute to drive out air and make the leaf flaccid, then in spirit to remove the chlorophyll (which is soluble in alcohol), and finally placing it in a saucer containing dilute iodine solution, which will either stain the leaf yellow, if no starch is present, or various shades of blue, if it is. When the absence of starch has been demonstrated, a plant is placed under each bell-jar, one of which (that provided with the soda-lime tube) also contains a vessel with some caustic potash solution. The bell-jars, &c., should stand on ground-glass plates, and the junction with the bell-jars must be made perfectly air-tight with vaseline. The caustic potash solution will absorb all the carbon-dioxide from the air in the bell-jar, and the fresh air which enters through the tube (A) is also deprived of its carbon-dioxide by the soda-lime, while the pumice of the other jar has no such action. It will be seen, therefore that under the conditions of this experiment one of the plants is being grown in an atmosphere free from carbon-dioxide and the other in a normal atmosphere, while both are provided with fresh air through the tubes (A, A′). The bell-jars, and contained plants, are placed in a bright light for a couple of days or so, and then the leaves are examined for starch by the iodine method described above. The leaves of the one grown in a CO_2-free atmosphere will be free from starch, while those of the other will contain it, so proving that in the absence of CO_2 in the air no starch is formed.

Nor can the place of the carbon-dioxide in the air be taken by carbonates in the soil ; this may be demonstrated by water culture, in which the solution contains, in addition to the constituents mentioned above, a small amount of carbonate of potassium. If a seedling is grown with its roots dipping into this solution, but with its leaves in an atmosphere free from carbon-dioxide, no starch is formed.

Several conditions are essential in order for the assimilation of carbon from the atmosphere to take place :—

i. **Light of sufficient intensity is required.** It can readily be shown by experiment that if two similar plants are taken and one exposed to strong light and the other to weak, the former will, after the lapse of a day or two, show much more starch in its leaves, and will increase in weight more rapidly, mainly owing to the more rapid assimilation of carbon. Starch is not the *earliest* product of carbon-

assimilation, as will be shown later, but as it is usually stored where rapid carbon-assimilation is taking place and is easily tested for, its amount is a useful indication of the activity of the process.

Moreover all the rays of light are not equally concerned in this process. To show this, **double bell-jars** are usually employed (Fig. 197); these are large jars with double walls enclosing a space, which is filled with a coloured fluid that allows only certain rays of the spectrum to pass through into the interior, in which a growing plant is placed, such as a young clover plant in a small pot. The space in the double wall of one jar is filled with potassium dichromate solution which allows only *orange* light to pass through, while that of the other is similarly filled with a deep *blue* liquid, made by adding ammonia to a solution of copper sulphate until the precipitate which is first formed is dissolved again. The two bell-jars are then exposed to bright diffused light for a day or two, and some of the leaves of the enclosed plants are tested for starch by the iodine method; the leaves of the plant grown in blue light will be found to contain little or no starch, while those of the plant grown in orange light will contain much more, showing that the less refrangible part of the spectrum (the yellow, orange and red end) is that concerned in carbon assimilation.

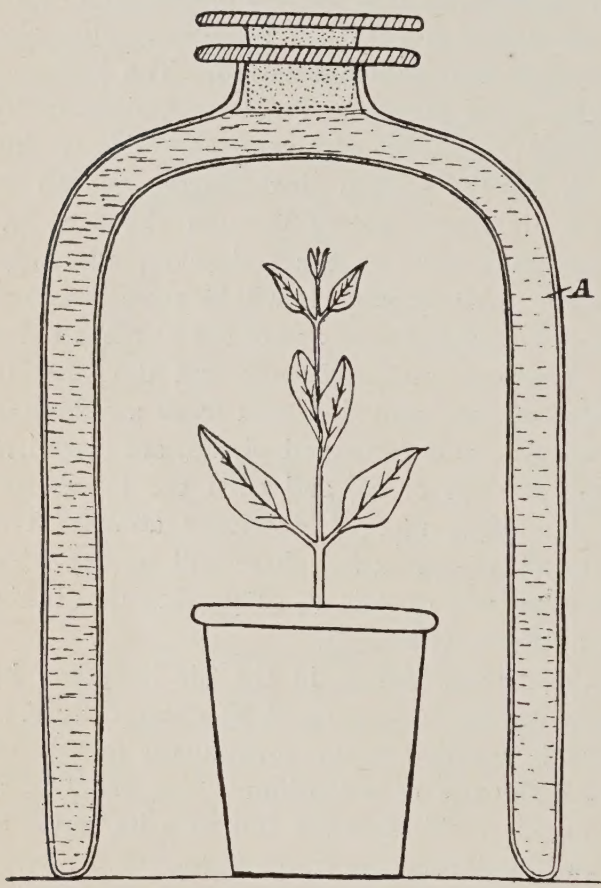


FIG. 197. Double bell-jar used for experiment to demonstrate the action of different coloured light in promoting carbon-assimilation. A=space containing a coloured liquid.

The starch which is formed by an actively assimilating organ, such as a leaf, during the day, disappears in darkness, owing to its conversion by a ferment (**diastase**) into soluble materials (sugar), and the subsequent transference of the soluble carbohydrate to other parts of the plant.

Moreover, even in a plant exposed to strong light carbon-assimilation, as shown by the storage of starch in the cells, only takes place in those parts which are actually exposed to light of sufficient intensity, and not in parts which are in any way protected. That the formation of starch is thus strictly localized may readily be demonstrated by partly covering the leaf of a Fuchsia, while it is still attached to the plant, with a sheet of tinfoil, which may be cut out in the centre in the form of a cross or other figure. The plant is then exposed to bright light for a day, and the leaf then removed, decolourized and tested with iodine; it will be found that only the parts actually exposed to light become blue, i.e. the central cross will be clearly marked out in blue, while the protected part of the leaf will be yellow, showing that starch is absent from that portion.

ii. **Chlorophyll is necessary.** The importance of chlorophyll has been already dealt with; a few details as to its formation and functions may be given here. Chlorophyll is in general only formed in the presence of light—plants grown in darkness do not become green but only yellow, and are said to be **etiolated.** A weak light is all that is required for this reaction (a much stronger light is required for the formation of starch), and the effect is produced by light rays of all refrangibilities. Exceptions to the rule are found in the case of certain Gymnosperms, such as *Pinus*, the seedlings of which become green even when germination takes place in complete darkness.

Oxygen is necessary for the formation of chlorophyll. This may be proved by putting an etiolated seedling (mustard answers well) in water contained in an inverted test-tube, and exposing to a bright light—the seedling does not become green because of the absence of free oxygen, while others placed on damp blotting-paper in the air soon develop chlorophyll.

A sufficiently high temperature is also necessary for the formation of chlorophyll, as is also a certain amount of iron salts in the food. If a plant is grown in a culture-solution which is destitute of iron, the first leaves formed may be green from the iron stored in the seed,

but the later-formed ones are white and are said to be **chlorotic**; that the absence of colour is due to the absence of iron, is shown by the fact that the addition of a few drops of a soluble iron salt (such as iron chloride) to the culture-fluid, prevents the chlorotic condition. Even when the latter condition has been assumed, the leaves may be made green by painting them over with a weak solution of ferric chloride.

If light is passed through a solution of chlorophyll and then examined with a spectroscope, the spectrum will be found to be crossed by a number of *dark absorption bands*, indicating that waves of certain wave-lengths do not pass through but are absorbed by the chlorophyll (Fig. 198). The principal absorption-band is in the red, and the **energy** which is thus obtained (light being a form of energy) is used by the protoplasm of the illuminated cells for the performance of **chemical work**, viz. the splitting up of the com-

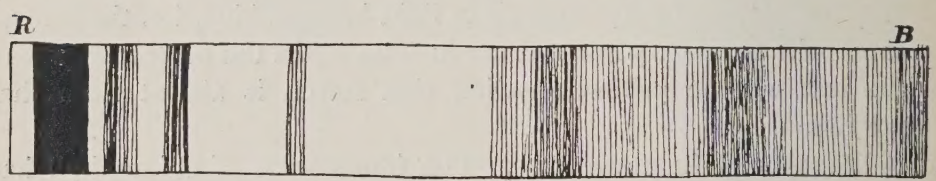


FIG. 198. The spectrum of chlorophyll obtained by passing white light (sunlight) through a solution of chlorophyll and then examining it with a spectroscope. R = the red end of the spectrum. B = the blue end of the spectrum. Several absorption bands are shown, some of which are at the blue end of the spectrum; the strongest band is in the red end.

paratively simple and stable molecules of carbon-dioxide and water, and the production from the elements of a more complex and less stable carbohydrate molecule. It thus appears that the function of the chlorophyll in carbon-assimilation is essentially that of an intermediary between the protoplasm which does the work, and the light which is the source of the energy by which the work is performed. *Protoplasm without chlorophyll is incapable of making use of the energy of the sunlight for the purposes of carbon assimilation.*

iii. **A sufficiently high temperature** is necessary for carbon-assimilation, as it is also for all the other active processes which go on in plants.

iv. **Carbon assimilation** and the consequent formation of starch, &c., does not go on if the cells are not supplied with *potassium salts* in solution. If a plant is grown in a culture-solution from which potassium is excluded, the plant remains stunted and no increase in weight takes place.

The exact changes which go on in an assimilating cell whereby, as an ultimate product, starch grains are formed in the chloroplastids, are only partly known. One result, however, is that the cell gives off oxygen gas, which passes into the air. This fact may easily be proved in the following manner: Take a number of shoots of a water-plant (such as *Elodea*) and place them in a cylindrical jar containing water. Spring water answers well, but not boiled water, as the plant requires dissolved CO_2. Now take a glass funnel, cut the tube short, and arrange it as shown in Fig. 199, so that the end of the tube is under water. Take a test-tube and invert it, filled with water, over the funnel. Place the apparatus in sunlight; bubbles of gas will escape from the plant, rise, and displace the water in the test-tube. When a sufficient quantity of the gas has been obtained it may be tested, and will be found to be oxygen.

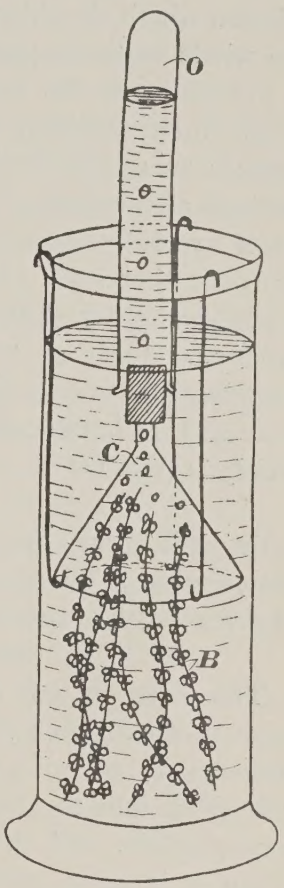


FIG. 199. An experiment to show the evolution of oxygen gas by a green plant during daylight. B = shoots of *Elodea*; C = bubbles of gas (oxygen) rising through the water from the leaves; O = oxygen gas collected in the test-tube.

An interesting experiment showing the evolution of oxygen during carbon-assimilation may also be performed with certain bacteria which are extremely sensitive to the presence of free oxygen. If such bacteria are mounted in water under a cover-glass and examined with the microscope, they will be found to swarm round any air-bubbles which may be present, and to collect round the edges of the preparation for the sake of the air (containing oxygen) which is there obtainable. Seal the preparation with oil to keep out the air, and after a time the bacteria cease their movement and come to rest. Now make another sealed preparation enclosing a filament of *Spirogyra*, and place it in the dark until the bacteria have come to rest; on exposure to light the bacteria will swarm round the green *Spirogyra* plant owing to the evolution of oxygen from its cells. It is possible to cast a spectrum on to such a preparation; if this is done, it will be found that the swarming of the bacteria is most active

where the filament is illuminated with red light, a result which we should be led to expect from a previous experiment (see p. 414), and from the position of the principal absorption band of chlorophyll (see p. 416).

It can be proved by experiment that during carbon-assimilation a green plant gives off exactly the same volume of oxygen as it takes in of carbon-dioxide ; this is interesting, because it is the numerical relation which should exist were the CO_2 decomposed into $C + O_2$ and the whole of the oxygen given off. This, however, as we shall learn, is probably not the case. The molecule of C which is thus set free might then combine with a molecule of water, H_2O, to form an organic substance having the composition of a carbohydrate. This method of formation is not, however, probable, as both carbon and water are substances having but little chemical activity. It is more probable that both CO_2 and H_2O are deoxidized, the former into *carbon-monoxide* (CO) and the latter into *nascent hydrogen* (H), so producing together the two atoms of oxygen represented in the equation and known by experiment to be given off. The CO and nascent H_2 would readily combine, and produce such a body as *formic aldehyde* (CH_2O)—

$$CO + H_2 = CH_2O.$$

Sugar is always formed as an early product in cells in which carbon-assimilation is taking place, and it is probably produced as the result of *polymerism* or *condensation* of the simple molecules first produced—

$$6\ (CH_2O)\ \text{(formic aldehyde)} = C_6H_{12}O_6\ \text{(grape-sugar)}.$$

The whole or part of the sugar so produced passes in the soluble form to the regions where growth is taking place, and is used for the manufacture of cell-walls and for other purposes ; the rest is generally converted into the insoluble form of starch by the chloroplastids or leucoplastids, and stored as such until such time as it is required, when it is again converted into the soluble form of sugar and by diffusion conveyed to the place where it is wanted.

The ten essential chemical elements of plant-food are *carbon*, *oxygen*, *hydrogen*, *nitrogen*, *sulphur*, *phosphorus*, *potassium*, *magnesium*, *calcium*, and *iron*.

Oxygen is absorbed in the free condition in connexion with the respiration of plants (p. 436) : also as CO_2 during carbon-assimilation, as water (H_2O), and as sulphates, nitrates, &c., from the soil.

Hydrogen is taken in mainly as water ; it is also contained in the complex organic compounds which constitute part of the food of non-green plants.

Nitrogen is taken in by most green plants from the soil in the form of *nitrates*. It is probable that ammonia-compounds (such as sulphate of ammonia) are not used as such by green plants, but must first be oxidized to nitrates. Certain *nitrifying bacteria* which are present in the soil are able to bring about this change, first converting the ammonia-compounds into nitrites and the latter by further oxidation into nitrates. Non-green plants (fungal and other parasites and saprophytes) also make use of more complex nitrogen-containing carbon-compounds.

Nitrogen is only exceptionally absorbed in the free form from the atmosphere (see p. 420), and most green plants will die in soil which is free from nitrates or other compounds containing nitrogen, notwithstanding that they are surrounded by the free nitrogen of the atmosphere.

Sulphur is one of the constituents of protoplasm and is obtained from the sulphates in the soil.

Phosphorus is also a constituent of protoplasm, especially of the nucleus. It is obtained in the form of phosphates from the soil.

Potassium is also obtained from the soil in the form of salts (carbonate, sulphate, &c.), and is necessary for the assimilation of CO_2 from the air (see p. 416). Roots, tubers (such as the potato), &c., in which storage of starch or sugar takes place, are usually rich in potassium salts of the organic acids, such as potassium citrate, potassium tartrate, &c.

Magnesium is absorbed from the soil in the form of nitrates, sulphates, &c. Although its presence is essential its exact use is not known.

Calcium, like magnesium, is absorbed as sulphate, nitrate, &c., from the soil.

Iron. See p. 415.

The use of calcium, phosphorus, potassium, and magnesium is difficult to understand. These elements are present in plant protoplasm in very minute quantities, but yet in their absence from the food of plants, although the other necessary constituents are present, the plant dies of starvation. We can at present only interpret these results by conceiving that these substances in some way profoundly influence metabolism.

Many other elements are commonly found in plants, but experimental culture has shown that they are not essential for their healthy development. **Sodium** is one of these and is found everywhere.

Silicon is deposited (as silica) in considerable quantity in the cell-walls of many grasses, and in *Equisetum*, &c.; it is absorbed from the soil in the form of silica (SiO_2), but is not essential as food, though it is probably useful in hardening the walls of the cells in which it is deposited and thus serves to keep off parasites. **Chlorine** is always present in plants, and is said to be essential in the case of buckwheat, but this is certainly not the case with most plants. **Bromine** and **Iodine** are present in most marine algæ, &c.

Special Modes of Nutrition in some Phanerogams.

i. Assimilation of atmospheric nitrogen by plants belonging to the Leguminosæ.

As already mentioned, most green plants die in soil which is free from nitrates, or from other nitrogen compounds which may be converted into nitrates by the nitrifying bacteria. An important exception to this rule is found in the *Leguminosæ*, which flourish in soil that is absolutely *free from nitrogen compounds of any kind.* Indeed the growth of these plants will actually enrich a soil in nitrogen, and in some places leguminous crops are cultivated for this purpose for the benefit of later-grown plants. If a clover or other leguminous plant is pulled up, the roots will be found to be covered with small swellings or **tubercles**, which are formed by the plant as a result of attack by a fungus in the soil (supra, p. 12). The exact nature of this fungus is at present undecided, but it is believed to belong to the bacteria: anyhow the cells of the swellings contain branches of a fungus-mycelium, from which small bodies (*gemmules* or *bacterioids*) are budded off and escape to infect other roots. In some way or other this fungus is able to make use of the free nitrogen of the air around the roots, and to convert it into compounds which are absorbed by the roots of the green plant. *Experiment has shown that it is only when this fungus is present in the soil that the tubercles are developed, and that free nitrogen can be assimilated only after the swellings have been produced.*

It is probable that the fungus lives in a **symbiotic condition** with the green plant, i.e. that each derives benefit from association with the other, the green plant being enabled to live in a soil which would otherwise be too poor in nitrogen, and the fungus receiving in return some of the carbohydrates which the cells of the tubercles contain in abundance.

ii. Partial or complete parasitism and saprophytism.

A considerable number of phanerogamic plants have become adapted to conditions in which they obtain either the whole or a part of their carbon, as well as the other elements, in the form of complex carbon compounds, either from other living plants (**complete** or **partial parasitism**) or from decaying organic matter (**complete** or **partial saprophytism**). Where only a part of the carbon is so obtained, the rest is assimilated from the atmosphere in the ordinary way by green leaves, &c., but the completely parasitic or saprophytic condition is accompanied by an absence of chlorophyll.

The mistletoe. This is perhaps the best known of phanerogamic parasites, and is found on a number of trees, especially the apple, black poplar, some firs, &c. Its white berries, which are covered with a viscid pericarp, are carried and deposited on the branches of trees by birds—especially the thrush—and there the single seed germinates, and soon forms from the radicle a flattened disc which serves to attach the seedling firmly to the branch of the host (i. e. the tree on which it lives). From **the attachment disc** a process now begins to grow through the bark, cortex, &c., as far as the surface of the young wood of the host; this process is called a **sinker** and it is of the nature of a root. During the next season the tip of the sinker becomes enclosed in the young wood of the host which is being formed by the cambium, while the sinker itself grows in length by an amount equal to the thickness of the annual ring of wood investing its apex: this process takes place year after year, so that in an old specimen the sinker may be seen to be embedded in a considerable number of annual rings of wood through which it appears to have forced itself. A zone of living cells of the sinker is always found just outside the young wood of the host, and from this region branches (**cortical roots**) arise and grow in length parallel to the long axis of the branch; from these cortical roots fresh sinkers arise and become enclosed in the wood, exactly as did the sinker formed in the first

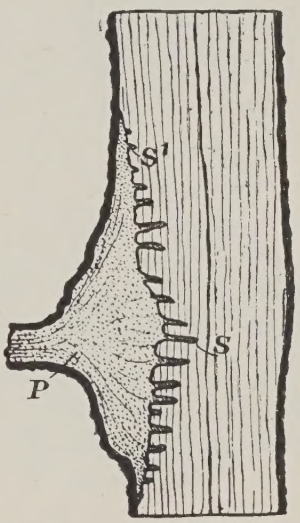


FIG. 200. Semi-diagrammatic representation of a branch attacked by the mistletoe. P = the parasite; S = the first-formed sinker; S′ = one of the latest formed sinkers.

place from the embryo. While this development of an elaborate absorptive system is going on within the tissues of the host, green stems and leaves are produced outside, the amount of the aërial development being dependent on the supply of nutriment taken up by the sinkers. Adventitious buds may be also produced from the cortical roots; these later swell, burst through the bark, and form new mistletoe-plants.

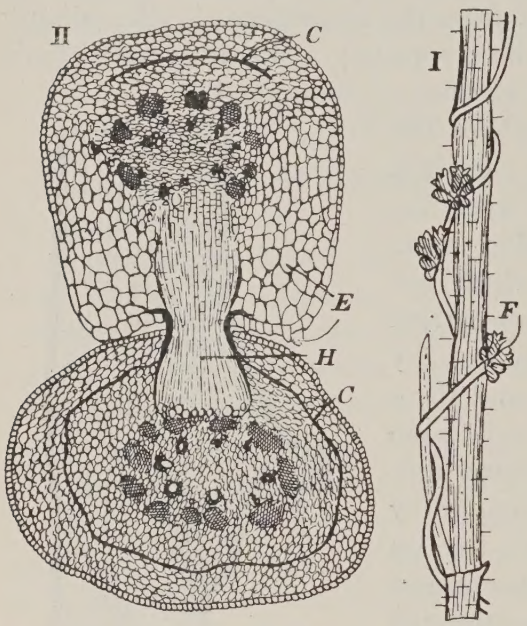


FIG. 201. The Dodder (*Cuscuta*). I. The parasite winding round the stem of a hop-plant. F = groups of flowers. II. Transverse section of parasite and host-plant, showing the penetrating haustorium (H). C, C = crushed cortical cells forming a complete ring in the host, but only occurring on the outer side of the parasite. The crushing is due to the penetration of the haustorium, which is also surrounded laterally by crushed cells. E = enlarged epidermal and cortical cells of the parasite.

The mistletoe, being a green plant, is only partly parasitical, as its chlorophyll-containing leaves assimilate in the ordinary way.

The dodder (*Cuscuta*). This genus of climbing parasitic plants belongs to the *Convolvulaceæ*, and commonly attacks clover, flax, heath, nettles, hops, &c. The plants are destitute of chlorophyll, and their fine reddish stems bear only small scale leaves and clusters of globular flowers.

The seeds of the dodder, which contain, as is usual in parasitic plants, a very rudimentary embryo, germinate on the ground, and send out a small club-shaped root into the soil; this germination takes place late in the spring, after the plants around have had time to start their growth and so provide supports up which the parasites may climb. The stem, while still enveloped in the seed-coat, grows at the expense of the reserve food-material in the root into a long thin thread which moves round in a circle (circumnutates, see p. 465), and may so bring itself into contact with a suitable host-plant, around the stem of which it at once begins to twine. Where the dodder is pressed against the support it develops peculiar attaching organs (**haustoria**), through which a vascular bundle, consisting of a few spirally thickened vessels

surrounded by rows of parenchymatous elements, passes and forces its way into the host from which the food supply of the parasite is now obtained (Fig. 201). The lower part of the stem, below the first haustorium, now dies away, so that the parasite becomes completely disconnected from the soil.

Haustoria of this kind are commonly regarded as adventitious roots, but as they are developed from the young cortex (periblem, pp. 70 and 75) and not from the pericycle they are best regarded as emergences.

As the dodder possesses no chlorophyll and is disconnected from the soil, it must obtain the whole of its nourishment from its host, and it is therefore **completely parasitical.**

Root parasites. A number of plants belonging to the *Scrophulariaceæ* (*Bartsia*, eyebright, yellow rattle, red rattle, cow-wheat, see p. 393) and to the *Orobanchaceæ* (broom-rape, toothwort) have suckers or haustoria on some or all of their roots, by which they attach themselves to the roots of other plants growing near them. The haustoria here (as in *Cuscuta*) are emergences and not real roots. Some are green (e. g. cow-wheat and the other *Scrophulariaceæ*) and have ordinary rootlets as well as the modified ones, and so are only partial parasites, while others (e. g. broom-rape) have no chlorophyll nor independent roots, and are therefore complete parasites. The common toothwort (*Lathræa squamaria*) is parasitic on the roots of trees, especially the hazel, ash, &c. The fleshy underground stems are closely set with fleshy white scale leaves (Fig. 203, I). From the stems arise adventitious roots which branch and then develop suckers (haustoria) at their ends, which are attached to and penetrate the tissues of the host-plant (see also p. 427).

Saprophytes. As with the parasites, so here, chlorophyll may be either present or absent. As examples of saprophytes with chlorophyll we may mention the twayblade (*Listera*), *Ericaceæ*, and *Pyrola* (wintergreens), which live in the peat on moors, or in the decaying leaves, &c., forming the soil of a forest. Among phanerogams which are destitute of chlorophyll and which live as saprophytes we have the yellow bird's-nest (*Monotropa*), an uncommon British plant which may live also as a root parasite; the bird's-nest orchis (*Neottia Nidus-avis*); coral-root (*Corallorhiza*), &c.

iii. Absorption of carbon compounds from the soil. It has been found that a great many forest trees, especially those belonging to the *Cupuliferæ* (p. 403), have a scantily developed root-hair system, but have their young roots covered with fungal hyphæ forming a kind of

feltwork known as mycorhiza. Such plants not only make use of the carbon-dioxide of the air as a source of carbon, but also use the decomposing organic matter, which contains carbon as well as other elements of the soil; the absorption of these complex carbon-compounds is believed to be favoured by the presence of the fungal hyphæ, while at the same time the fungus is probably partly nourished by the tree—so that we have here another example of **symbiosis** or **mutual advantage** (see p. 420).

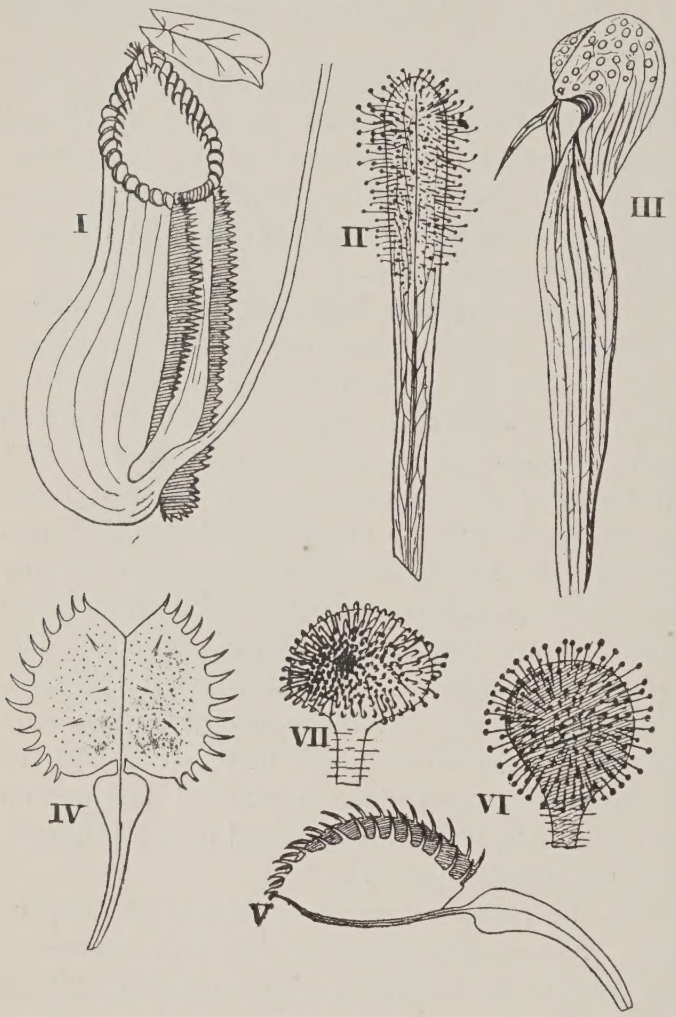


FIG. 202. Carnivorous plants. I. Pitcher of *Nepenthes*. II. Leaf of *Drosera longifolia*. The upper surface of the end of the leaf is covered with the characteristic tentacles, each with a glandular apex. III. Ascidium of *Darlingtonia*. IV. Leaf of Venus's Fly-trap (*Dionæa*) in the open condition. V. Ditto, closing. VI. Leaf of *Drosera rotundifolia*, seen from above, showing the tentacles in the expanded condition. VII. Ditto, with the tentacles bent over to an object near the centre of the leaf.

iv. Carnivorous or insectivorous plants. A number of plants are provided with special arrangements for the capture, digestion, and absorption of insects, so obtaining a part of their nitrogenous food in an altogether peculiar manner.

A familiar British insectivorous plant is the sundew (*Drosera*), commonly found in damp mossy hollows (Fig. 202, II, VI, VII). Three British species of *Drosera* are recognized, but the commonest is *D. rotundifolia*, a form with horizontal orbicular leaves covered on the upper surface with long sticky hairs or tentacles, each with a glandular

apex. The tentacles vary in length, those at the margin of the leaf being the longest. The small drop of secretion at the apex of each tentacle looks very bright in the sunlight—hence the popular name of sundew. When a small insect, such as a midge, a small beetle, or an ant, alights on the surface of a leaf it is held by the viscid secretion formed by the glandular tentacles, and its struggles to free itself only result in it getting more and more entangled and covered with the secretion, while at the same time the stimulus set up by contact with some of the tentacles travels to the others, with the result that they bend over to the place where the insect lies (Fig. 202, VII). The secreting heads of the tentacles are thus brought together over and around the body of the insect, which becomes enclosed in the secretion and dies from suffocation. The secretion also becomes acid, and is found to contain a ferment similar in nature to the pepsin of the gastric juice of animals, so that a true digestion of the nitrogenous part of the insect's body is effected, all indigestible portions being left behind. The digested part is absorbed, together with the digestive fluid itself, by the glandular ends of the tentacles, and these are finally left in a dry condition, so that the indigestible remnants can be blown away by the wind. After a day or two the viscid drops reappear at the ends of the tentacles and the leaf is again in a condition to catch insects. The movements of the tentacles, digestion, &c., may also be brought about by placing small pieces of meat, cheese, or anything nitrogenous on the leaves; grains of sand, sugar, or other non-nitrogenous material also cause movements of the tentacles.

Venus's fly-trap (*Dionæa*) also belongs to the *Droseraceæ*. It is restricted to the moors of a patch of country lying along the east coast of N. America. It exhibits one of the most curious adaptations for the capture and digestion of insects. The leaves are arranged in a rosette around the flowering axis as in *Drosera*, and each consists of a flattened petiole terminated by a roundish lamina (Fig. 202, IV, V). The latter is fringed by a number of long stiff teeth, and is traversed by the midrib, on which the two halves of the lamina can turn as on a hinge. The upper surface of the lamina is dotted over by a large number of glands on short stalks, and each half also carries three long bristles near the centre, which are hinged to the surface of the leaf by pads of parenchymatous tissue. When an insect crawls or alights on the leaf and touches one or more of the central bristles, the lobes of the lamina instantly fold together like the closing of a book, so enclosing the insect within them. The stiff teeth at the margin interlock and

prevent any possibility of escape, while the glands, which were before dry, now begin to pour out a secretion containing an acid and a ferment which dissolves the body of the animal, leaving only the indigestible parts behind. The matter, including the secretion itself, is absorbed by the glands, which again become dry, and the trap reopens. Irritation of any kind (whether the irritating object is inorganic or organic, non-nitrogenous or nitrogenous) will cause the closure of the valves, but unless the body is nitrogenous the leaf soon opens again. In the latter case the leaf usually remains closed from a week to a fortnight.

The butterworts (*Pinguicula*) include the British form *P. vulgaris*, occurring in damp places in hilly districts. The plants have rosettes of entire fleshy leaves covered with small glands which secrete a true digestive fluid. The edges of the leaves are turned up so that each is converted into a shallow trough covered with the viscid secretion of the glands. If an insect, or any nitrogenous body, comes in contact with the glands at the margin of a leaf, the edge rolls slowly inward and closes over it and digestion gradually takes place. After digestion and absorption are completed the edge unrolls again. Small pieces of cartilage placed on the leaf are digested, and milk is coagulated and digested.

The pitcher-plants are perhaps the best known of all carnivorous plants, though none of them are British. The tropical genus *Nepenthes* consists of between thirty and forty species which are found growing on the marshy ground around pools, &c., over which the pitchers hang. Each leaf consists of a flattened petiole, passing into a kind of tendril, which may coil itself around the branch of a tree or other object, and which finally ends in the pitcher, which is generally regarded as a hollowed-out portion of the petiole (Fig. 202, I). The pitcher is surmounted by a lid which probably represents the lamina of the leaf. The pitcher and its lid are brightly coloured and serve to attract insects, and the attraction is increased by the secretion of honey on the under surface of the lid and around the mouth of the pitcher. The interior of the pitcher itself is bright and smooth, and insects slide down into the secretion which occupies the lower part of the vessel. Sometimes the rim is provided with stiff, downwardly directed bristles, which form an additional safeguard against the escape of crawling insects, while a flying insect would probably strike against the lid and be projected back again into the pitcher. The liquid that partly fills the pitcher has an acid reaction and contains

a ferment; it is secreted by special glands which lie on the inner surface of the pitcher. The digested material is absorbed by special cells which are situated towards the lower part of the pitcher. The *Cephalotus* of eastern Australia also has pitcher-like leaves, while *Sarracenia* and *Darlingtonia* (Fig. 202, III) of N. America have long narrow pitchers or ascidia, containing fluid in which the captured organisms are decomposed by the microbes which abound in the fluid.

The common toothwort (*Lathræa squamaria*) has already been described as a root parasite (p. 423); it is also to a certain extent carnivorous. The fleshy underground leaves are rolled round, and

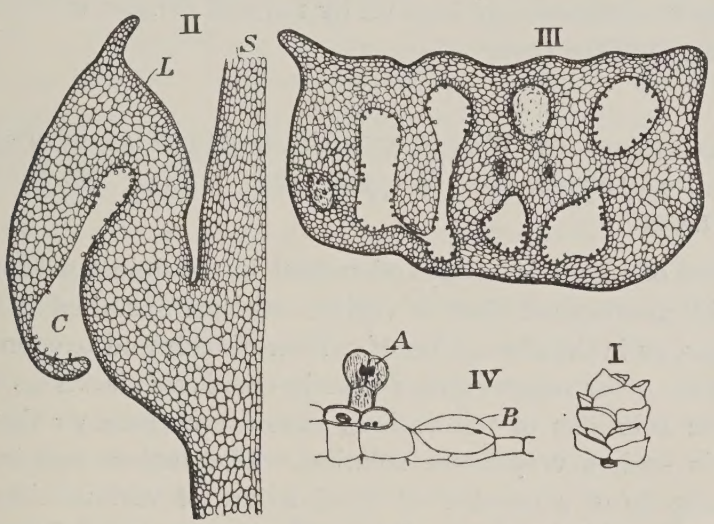


FIG. 203. The Common Toothwort (*Lathræa squamaria*). I. Portion of underground stem covered with thick fleshy leaves. II. Vertical section of leaf and part of stem, showing one of the chambers in which small organisms are caught. C = chamber; L = fleshy leaf; S = stem. III. Vertical section of leaf cut at right angles to II, showing a number of chambers. IV. Inner surface of chamber, showing one of the peculiar stalked cells (A) from which protoplasmic filaments are protruded, also one of the tabular cells (B).

each encloses a number of chambers, into which insects and other small organisms in the soil can pass (Fig. 203, I, II, III). The walls of these chambers exhibit peculiar structures, each consisting of a little head of two cells supported on a unicellular stalk (Fig. 203, IV, A); from the head-cells delicate protoplasmic filaments are protruded which come into contact with the intruders. Other peculiar tubular cells also occur among the cells of the inner surface, and there seems little doubt that the whole apparatus constitutes a trap for the capture of small organisms, and that the plant normally obtains a part of its food in this way.

The bladderworts (*Utricularia*) belong to the same order as the

butterwort. There are several British species, all of which are aquatics without true roots. They have much-divided submerged leaves furnished with small bladders (modified leaflets) in which small organisms are entrapped. Each bladder has a kind of trap-door opening inwards only, so that an insect when once in finds great difficulty in getting out again. The nutritive material resulting from the decay of the organisms is sucked up by special absorption-cells scattered over the inner surface of the trap. What it is that induces insects to enter is not known : it may be for food or protection. Most of the organisms captured are small crustaceans (*Cypris*, *Daphnia*, &c.) ; larger organisms are kept off by the stiff bristles which surround the opening into the trap.

The Absorption of Water and Food-material by the Roots and Circulation of Water and other Materials in the Plant.

The food of plants is always absorbed in the fluid condition, either as a liquid, as when solutions of various salts are absorbed by the roots, or as a gas, as in the absorption of carbon-dioxide and oxygen from the atmosphere. Our water-culture experiments have shown us that only very dilute solutions of the various salts are necessary : the water in the soil is such a very dilute solution. The surface soil is in most cases made up of a number of small stones of various sizes derived from the subsoil below and mixed with finer material formed partly by the decay of plants, and the interstices between the solid particles are occupied by air (the 'ground air') containing the oxygen which is necessary for the respiration of the roots (p. 436). Normally the particles of the soil are each surrounded by a pellicle of water containing various salts in solution, but under some conditions, as during heavy rain, the spaces between the particles become filled with water and the ground air is driven out, producing an unhealthy condition for the plants growing in it because respiration by the roots is then stopped. The development and function of root-hairs have already been described (p. 67) ; these come into the very closest relationship with the particles of the soil and their surrounding pellicles of water, and so closely do they adhere that it is often impossible to separate them without breaking the delicate root-hairs. If a growing plant is repotted it nearly always droops for a few days after the change, simply because the transference results in damage to the root-hair

system and consequent loss of power to absorb more water from the soil, until the formation of new root-hairs allows the plant to make good the loss of water which is constantly taking place from the leaves, &c.

The walls of the root-hairs are very delicate and thin, and within them lies a thin layer of granular protoplasm surrounding the large central vacuole filled with cell-sap, so that the watery solution of various salts *outside* the root-hair is only separated from the vacuole *inside* (which also consists of a watery solution of various substances) by the thin cell-wall with its delicate protoplasmic lining.

But what causes the water and the dissolved salts to pass through this double membrane from without inwards? A simple experiment may perhaps serve to illustrate one or two points in connexion with root absorption. Take a large thistle-headed funnel or a 'dialyser' (Fig. 204), and tie a piece of bladder or 'vegetable parchment paper' over the expanded end; the thistle-head and a portion of the tube are now filled with a solution of common salt and the whole placed in a beaker of distilled water (Fig. 204). It will be found that after a time the level of the salt solution in the funnel-tube will rise, showing that water has passed through the bladder; while if the water in the beaker is tested with silver-nitrate it will be found to give a white precipitate, showing that some of the salt has also passed through the bladder; it is clear, however, from the fact that the level of the salt solution in the tube has risen, that more water has passed inward than salt solution outward. This experiment demonstrates that solutions of some solid substances (e.g. common salt) will pass through a *closed membrane*, and also that the presence of common salt in solution exercises a powerful influence in causing the absorption of more water from without. A similar experiment may be performed by using a solution of sugar instead of salt; after a time the sugar can be detected in the water in the beaker, showing that sugar also is capable of passing through a closed membrane. If, however, the experiment is tried with a solution of starch, and after an hour or two the water is tested with iodine solution, no blue colouration results, showing that starch cannot pass or diffuse through the bladder. Salt and sugar are therefore said to be **diffusible bodies,** while starch is **indiffusible,** and the physical process by which the substance passes through the membrane is described as **osmosis,** which may be defined as '*diffusion through a membrane.*' The process by which water and food-substances in solution pass through the walls of a root-hair is probably somewhat

similar ; the double wall of cellulose and protoplasm forms a permeable membrane, through which substances which are *both soluble and diffusible* may pass, while the cell-sap holds certain materials in solution, among which the most important are probably the organic

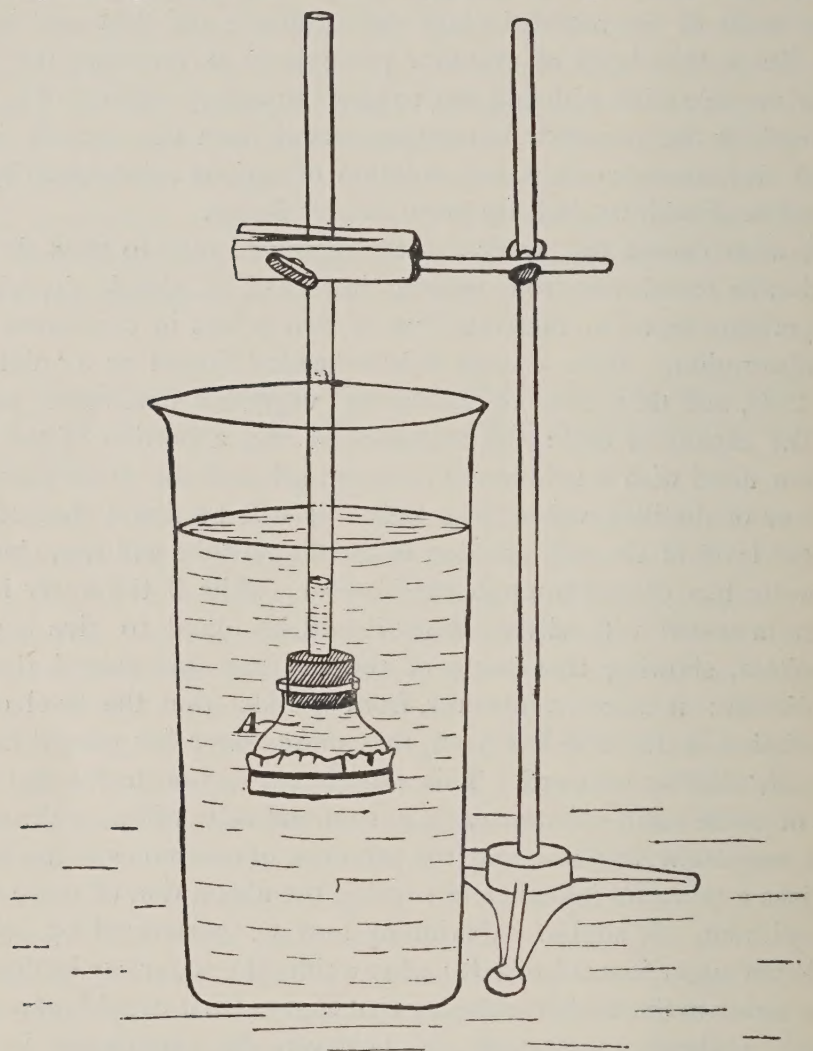


FIG. 204. An experiment to illustrate osmosis. The dialyser (A) is closed at the bottom with vegetable parchment paper and is connected above with a fine glass tube. The dialyser and part of the tube are filled with salt solution and suspended in a vessel containing pure water. After a time the level of the salt solution in the tube will rise, showing that water has been absorbed. At the same time a small quantity of the salt passes through into the water in the beaker.

acids, capable of causing the absorption of water, just as did the salt in our first experiment.

But although absorption is to a certain extent a purely physical process, it is by no means entirely so, since the lining layer of protoplasm

exercises an important controlling influence on the interchange which takes place between the cell and the surrounding fluid.

It must not be supposed that the substances in solution in the soil water are necessarily absorbed in the same proportion as they occur in the water outside the plant, i. e. that the watery solution which passes through the walls into the cells is necessarily of the same composition as that outside. The *absorption of material in solution is selective*: any indiffusible soluble or insoluble substance is not absorbed, nor is any substance of which an equivalent quantity is already present in the cell-sap. If therefore a substance is absorbed which accumulates in the cell-sap and is not chemically altered, its further absorption will soon cease; whereas a substance which undergoes chemical change ceases to exist as such in the plant, and its absorption may go on continuously.

Different plants grown in the same soil may severally absorb the constituents of the soil water in very different proportions, as may be determined by analysis of the ash left after all the organic matter has been burnt away; thus grasses and a few other plants absorb large quantities of silica from the soil, whereas most other plants, even when growing in the same medium, absorb very little, a difference which depends on the fact that grasses are able to remove the silica from solution and deposit it in their cell-walls. To sum up, then: it is important to distinguish clearly between the *absorption of water* and the *absorption of the substances held in solution*; the former process may go on without the latter, and is brought about by the presence of osmotically active substances, such as the organic acids, in the cell-sap, while the absorption of the substances in solution depends on their diffusibility and on the changes which they may undergo in the plant after absorption.

Substances may be absorbed by the roots which are known to be insoluble or nearly so in pure water, e. g. calcium carbonate, certain silicates, calcium phosphate, &c. The soil water is never pure, but always contains carbon-dioxide in solution, and this renders the calcium carbonate and silicates soluble; sodium or ammonium chloride in solution will render calcium phosphate soluble; while the sap which exudes to a certain extent from the root-hairs has an acid reaction due to the presence of organic acids. We can demonstrate this latter fact by allowing a plant to grow in a thin layer of mould over a slab of polished marble ($CaCo_3$) so that the growing roots come into contact with the latter; after a time it will be found that the acid sap exuded

through the root-hairs has etched the surface of the marble where the roots have been in contact with it, i. e. the marble has been dissolved. The water and other food-materials thus absorbed into the root-hairs pass inward, and are distributed to the cells of the cortex by a similar process of osmosis from cell to cell.

The long aërial roots of epiphytic orchids and aroids possess a curious and important adaptation for obtaining water from the air. No root-hairs are as a rule developed, but the root is covered with a thick white coating known as the **velamen**, consisting of empty partly lignified cells with delicate thickening bands on their walls (Fig. 205). The walls of these cells are perforated in places between the bands, and the tissue sucks up any water which falls on the roots as rain, or is deposited as dew, like a sponge. It is said that the velamen has also the power of actually condensing the water-vapour in the air.

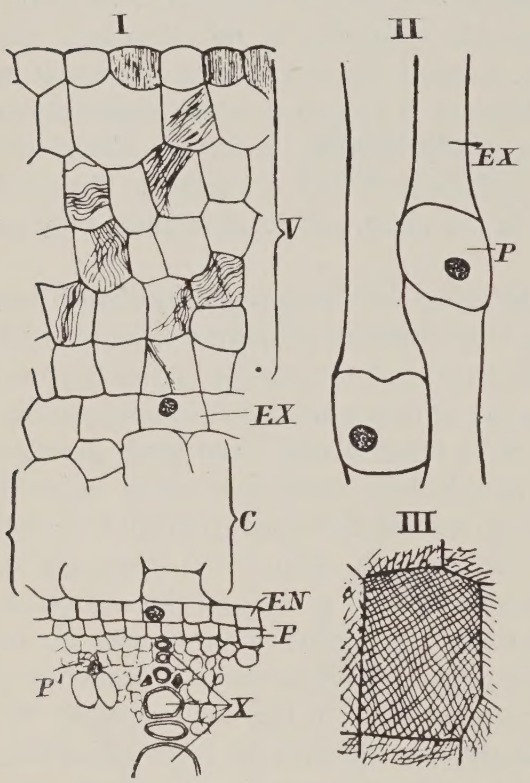


FIG. 205. I. Transverse section of root of *Oncidium* (an orchid). C = cortex (greater part omitted); EN = endodermis, with passage cell opposite the protoxylem elements; EX = exodermis, with passage cell showing nucleus; P = pericycle; P′ = phloem; V = the velamen; X = xylem. II. Tangential section of the exodermis. EX = ordinary cells of the exodermis; P = passage cell with large nucleus. III. Velamen cell with thickening bands on its walls.

The cortex, which lies within the velamen and often contains chlorophyll, is bounded internally by the endodermis and externally by a layer of similar cells known as the **exodermis**; both of these layers show a number of 'passage cells' (Fig. 205, I, II), with thin unlignified walls through which the water absorbed by the velamen can pass to the central xylem elements.

The subject of the absorption of water brings us to another important one—that of **turgescence**. If we take a small bladder, or one of the skins used in making sausages, and half fill it with a strong solution of

common salt, and tie it up and put it into a vessel of pure water, it will gradually swell out until it is filled owing to the absorption of water from without. The absorption of water is due to osmosis, and the osmotically active substance, in this case, is common salt. A living plant-cell, moreover, is capable of taking up so much water that it causes stretching of the elastic wall, resulting in considerable pressure between the cell-wall and the cell-sap; and such a cell is described as being **turgid** or in a **state of turgescence**. Three conditions are necessary in order that a cell may become turgid: (1) the presence of *osmotically active substances* in the cell-sap to cause absorption of the water, (2) the presence of a layer of *living protoplasm* to prevent the escape of the water as the pressure increases, and (3) the presence of an *elastic cell-wall* which on being stretched exerts pressure on its contents. It is the absence of the second of these conditions which precludes the possibility of turgidity in a dead cell.

It is to turgidity that the stiffness of herbaceous members is mainly due. The leaves on a cut branch wither because the cells lose their turgidity owing to loss of water; they become stiff and fresh again if the cut end of the branch is placed in a vessel of water, simply because the absorption of water enables the cells to regain their original condition of turgescence.

Turgidity may also produce *strain or tension between neighbouring tissues*. To demonstrate this we can take a long internode from a fresh straight stem of the elder in spring, when growth is rapid, and measure its length; we next remove a narrow strip of the cortex and measure this, and it will be found to be slightly *shorter* than the original length, showing that it had been in a stretched condition; now remove the whole of the tissue outside the pith and measure the length of the latter, and it will be found to be *longer* than the original length, showing that it had been compressed. Next place the pith, which in this young condition consists of *living* cells, in a vessel of water and after an hour or so again measure its length; it will be found to be much longer than before, a result brought about by increased turgescence and consequent increased length of the constituent cells. In an experiment the following figures were obtained :—

Original length of internode	17·5 cm.
Length of removed slip of cortex	17·4 cm.
Length of removed pith	17·7 cm.
Length of pith after soaking in water for $1\frac{1}{4}$ *hours* .	18·2 cm.

If the elongated pith is now soaked for some time in a fairly strong

solution of common salt it becomes short again, because the salt solution draws water from the cells and they lose their turgidity.

The phenomena attending the withdrawal of water from cells may be also observed with the microscope. Cut thin sections (not too thin, as it is necessary for some cells to be unopened) of the common beet-root, rinse in water and mount on a slip in water. The microscope will show that each cell contains a thin layer of protoplasm, which surrounds a large central vacuole filled with coloured cell-sap. Run in under the cover-glass some $2\frac{1}{2}$ per cent. common salt solution and watch the result; water is abstracted from the central vacuoles of the cells by the action of the salt solution, and as the vacuoles diminish in size the lining protoplasm follows, so that the greater part of it leaves the cell-walls, to which it remains attached only at certain places. A cell in this condition is also smaller in size, since the cell-wall is no longer on the stretch; such a cell is said to be **plasmolysed**. Now irrigate the preparation with water so that the salt solution is removed; the cells regain their normal appearance and become turgid. If the water in which the preparation lies is heated to kill the protoplasm, the cells can neither be plasmolysed nor made turgid again, thus showing that these conditions depend on the *living* activity of the protoplasm.

Root Pressure. We have seen how the water, &c., absorbed by the root-hairs, passes from the latter into the cells of the cortex, which thus tend to become more and more turgid. After a time, however, the limit of the cells' turgidity is reached, and then a reaction is probably set up in the cells of the innermost part of the cortex, by which some of the cell-sap is forced into the adjoining xylem elements by the elastic contraction of the distended cell-walls. This method of escape of cell-sap from turgid cells is described as **filtration under pressure**. The water thus passed into the xylem vessels or tracheides is under pressure—**the root pressure**—as may be shown by the following experiment: Take a fairly large healthy plant of the vine, or other plant, in the spring, before the leaves have become fully functional, so that there is little transpiration of water, and cut it off close to the ground, keeping the cut end wet with water; arrange as shown in Fig. 206, taking care to bind the junction of the plant and the india-rubber tubing with wire so that it is quite air-tight. The apparatus (A) must next be completely filled with water, which must also fill the bottle (D) over the mercury, and the stopper (C) is then inserted. After a time the mercury in B will begin to rise, showing that water is being

forced out of the cut stem. If the experiment is kept up for some days, and especially if a vine-plant can be used (the phenomena are much more pronounced in the vine than in most other plants), a periodicity in the height of the column, after it has reached its maximum height, will be noticed, the height of the column in B being greatest in the afternoon and least in early morning. That the phenomenon is really due to *root* pressure may be proved by cutting the root off during the rising of the water, and allowing the lower end of the stem to dip into water—the water no longer rises, but at once begins to fall.

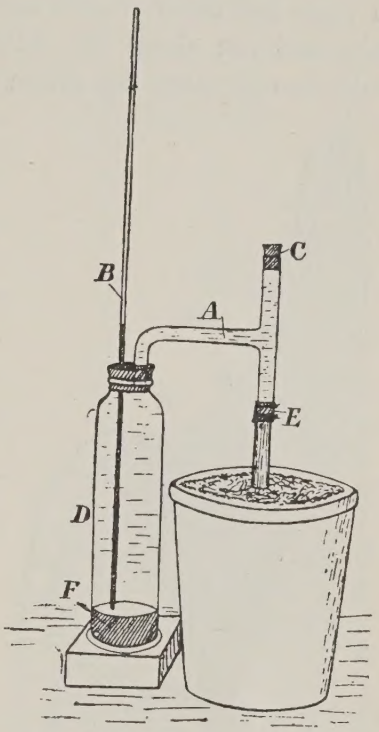


FIG. 206. Experiment to illustrate root-pressure. B = fine tube partly filled with mercury and dipping into the mercury in D; C = rubber stopper; D = glass bottle containing a little mercury (F) and then completely filled with water; E = strong rubber tube, which is tightly connected (by wire ties) to the cut end of the stem and to the glass apparatus A. There is free connexion between the water in D and that in A. When water is forced out of the cut end of the plant the pressure on the mercury in D is increased, and the column of mercury in B consequently rises.

Other evidence of root pressure is seen in the drops of water which exude from the leaves of many plants (e. g. grasses) at night, especially after a hot day. After a hot day the soil still remains warm while the air above is much colder; under these conditions transpiration may be practically stopped, while absorption by the roots is so active that the excess of water is forced out of the terminations of the vascular bundles in the leaves and appears as drops, either over ordinary stomata, special water-stomata, or fissures in the epidermis of the leaf (as in grasses). Water-stomata are found in *Tropæolum*, *Saxifraga*, &c.; they differ from ordinary stomata in that they excrete *drops* of water and not merely water-vapour, and that they are incapable of changing their form so as to close the aperture. In many *Saxifragaceæ* and *Crassulaceæ* the water-stomata are associated with chalk-glands (Fig. 207), and the water which is exuded is highly charged with carbonate of lime; this may be deposited on the surface of the plant to such an extent that effervescence takes place on treatment with an acid.

The 'bleeding' of certain plants (e. g. the vine) when cut in the spring is also a result of root-pressure.

Distribution of water and other substances. It has been already stated that the watery sap absorbed by the roots travels upwards along the xylem elements, and especially the vessels and tracheides. In trees the water travels along the latest formed wood or sap-wood only, and not along the older wood or heart-wood. That the water really travels along the xylem elements is most easily demonstrated by causing a shoot to grow in a solution of a dye (e. g. eosin) which will stain the tissues through which it passes; on afterwards cutting the stem across and examining it with a lens it will be seen that only the xylem is stained. Water readily passes in the radial direction along the medullary rays, and in the tangential direction through the thin membranes of the pits, which it will be remembered are usually confined to the radial walls of the elements on which they occur.

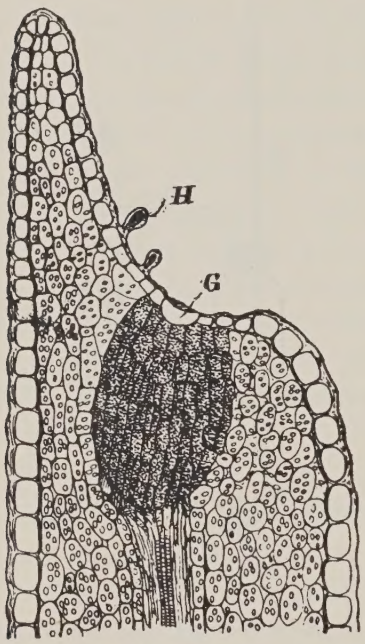


FIG. 207. Chalk-gland and water-stoma in *Saxifraga aizoon*. Section through one of the teeth of a leaf. G = one of the guard-cells, beneath which is the tissue (*epithema*) of the chalk-gland. The cells have dense granular protoplasm but no chlorophyll. Tracheides sheathe the base of the epithema and a vascular bundle runs up to it. H = hairs.

Carbohydrates in the form of sugar travel through the parenchymatous tissues, particularly those of the inner cortex just outside the endodermis. The endodermis itself often serves as a depository of starch, and this fact is made use of as a help in its identification.

Nitrogenous material travels in the form of soluble amides mainly through the sieve-tissue (phloem) of the vascular bundles.

The Respiration of Plants.

We have already seen that green plants in daylight absorb carbon-dioxide from the atmosphere and give out oxygen, a process which is the exact converse of that carried out during the breathing or respiration of animals, when oxygen is absorbed and given out again

in its oxidized condition of carbon-dioxide. It is important to know, however, that the peculiar process by which carbon is obtained by green plants is not the respiration of plants: respiration is practically the same process in all organisms, whether plant or animal, highly organized or simple, green or non-green, and is one by which the organism obtains the oxygen without which its activity as a living organism cannot go on. Respiration is continuous, day and night, and only ceases with death; it is masked, however, in green plants during daylight by the much more abundant evolution of oxygen which goes on in connexion with carbon-assimilation.

That plants do absorb oxygen and give out carbon-dioxide may be proved by some simple experiments. In order that the experiments may show the most marked results, plants or parts of plants which are undergoing rapid growth, such as germinating seeds, opening leaf- or flower-buds (dandelions, chrysanthemums, and other heads of composites answer well), are employed. If we allow some barley-grains to soak in water for twenty-four hours, and then, after removing the superfluous water, place them in a large wide-mouthed bottle provided with a well-fitting india-rubber stopper, which is allowed to remain in a dark place for a day or two, and test the gas in the jar with a lighted taper, the latter will be extinguished at once, showing the absence of oxygen.

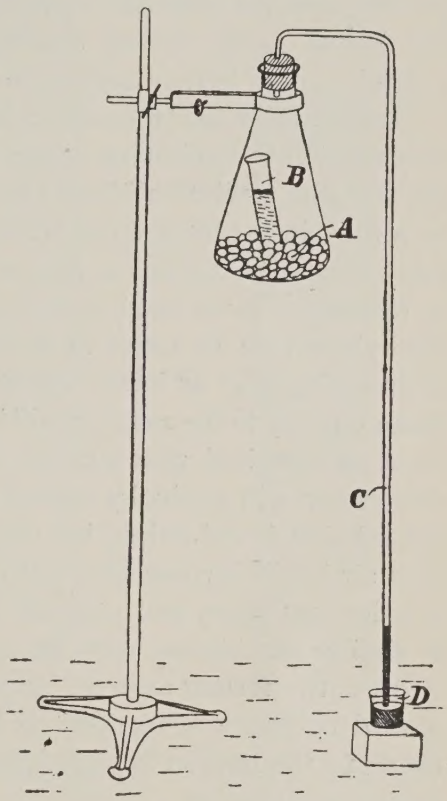


FIG. 208. An experiment to illustrate the respiration of plants. A = soaked barley-grains covering a piece of wet blotting-paper at the bottom of a glass flask; B = test-tube containing a solution of caustic potash; C = fine tube connected with the flask and dipping into mercury contained in a small vessel (D). The connexions with the flask must be air-tight.

A more exact experiment may be performed by using the apparatus shown in Fig. 208. The barley-grains in the flask absorb oxygen from the air and give out carbon-dioxide; the latter gas is absorbed by the caustic potash, so that the absorption of oxygen is indicated by the rise of the mercury in the fine tube.

Another good way of showing that CO_2 is produced in the respiration of plants is by drawing (by means of an aspirator) atmospheric air through a vessel containing some germinating peas or beans. The entering air must first be robbed of its CO_2 by passing it through a vessel (or vessels) containing baryta water, so that the air enters the vessel containing the germinating seeds quite free from CO_2. After passing over the peas the air is drawn through another vessel containing baryta water, which shows the presence of CO_2 by forming a precipitate of barium carbonate.

Prof. Farmer has recommended the use of a solution of *methylene blue* for simple respiration experiments [1]. The experiments depend on the fact that a solution of methylene blue loses its colour if acted upon by a reducing agent (i.e. one which abstracts oxygen), but if the colourless (reduced) solution is shaken up with air or oxygen the colour is restored. If we make a weak solution (about 0·0005 per cent.) of methylene blue in water in a large test-tube, and place in it some germinating peas or barley and keep them in the dark for some hours (from one day to the next), it will be found that the seeds are surrounded by a decolourized zone due to the abstraction of oxygen. The decolouration will gradually extend upward until practically the whole of the solution is colourless, but if some of it is drawn off and shaken up with air it will become blue again. If the peas are removed from the solution, cut open, and exposed to the air, they also will become blue. A similar experiment may be performed with branches of *Chara* or *Elodea* (the former answers better), which must be kept in the dark; after decolouration, exposure to light will bring back the blue colour, owing to the oxygen liberated in the decomposition of carbon-dioxide during assimilation.

Although a supply of free oxygen is a necessity for nearly all organisms, some plants, such as germinating seeds of the pea, &c., may be kept living for some time and will evolve CO_2, under such conditions that the absorption of free oxygen is impossible. Fig. 209 illustrates a simple experiment to prove this. A wide test-tube is filled with mercury and then inverted in a basin containing the same metal. The tube must be quite filled with mercury, and then about six or eight germinating peas, preferably without their seed-coats so as to avoid the possible introduction of air, are passed, one at a time, under the rim of the test-tube, of which they will occupy the upper end. The tube should now contain nothing but mercury and peas; allow it to

[1] See *Nature*, vol. lviii.

remain for about a day, and it will be found that a considerable quantity of gas has accumulated in the upper part of the tube. That this gas is CO_2 may be proved by introducing a little strong potash solution by means of a bent pipette, taking great care not to introduce air at the same time ; the gas is absorbed and the mercury rises again.

The evolution of CO_2 in the last experiment shows that respiration is taking place although the oxygen is not obtained from the air. The production of CO_2 by the cells, without the corresponding absorption of free oxygen (**'anaërobic respiration'**), can only go on for a short time, and in the absence of free oxygen most plants soon die for a reason which will be seen later.

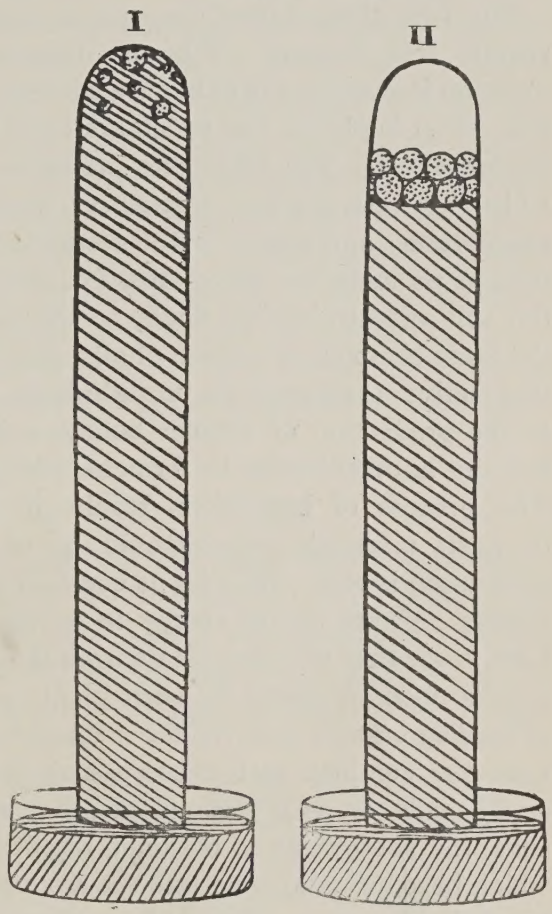


FIG. 209. Experiment to illustrate 'anaërobic respiration.' I. Inverted test-tube filled with mercury and peas and standing in a basin of mercury. II. The same after a day or two, showing the accumulation of CO_2 in the upper part of the tube.

Some fungi, however, will live without free oxygen for an indefinite period (e.g. yeast, pp. 266 and 275), and yet others (certain bacteria) are so peculiarly adapted to their condition of life that contact with free oxygen results in death. The yeast-plant will live either in the presence or absence of free oxygen and will produce its characteristic fermentative effects, but the growth of the yeast-plant itself, as shown by the activity of the budding process, is much less vigorous in the absence of oxygen. The CO_2 evolved in fermentation by yeast does not necessitate the absorption of oxygen, as both alcohol and CO_2 are produced by the decomposition of sugar, thus :—

$$\underset{\textit{Grape-sugar}}{C_6H_{12}O_6} = \underset{\textit{Alcohol}}{2C_2H_6O} + \underset{\textit{Carbon-dioxide.}}{2CO_2}$$

Succulent plants (such as Cacti, &c.) have been found, when kept in the dark, to absorb oxygen without giving out carbon-dioxide, i. e. the oxidized or partly oxidized carbon is not liberated in the form of CO_2, but is retained in the cells of the plant in a more complex condition.

But, with these exceptions, plants respire in the ordinary way and require free oxygen. Why is oxygen required? To answer this question it is necessary to inquire somewhat into the chemical processes that go on in plants, and which are collectively designated by the term **Metabolism.** The metabolic processes are of two kinds: (1) those which are essentially constructive (**constructive metabolism** or **anabolism**) and result in the formation of more complex materials, such as proteids, carbohydrates, &c., from simpler bodies derived from the soil and air, leading finally to the production of protoplasm itself, the most complex substance of all; and (2) those which are essentially destructive (**destructive metabolism** or **katabolism**) and result in the production of simpler bodies, either from protoplasm itself or induced in other bodies by ferments which are produced by protoplasm. The process of katabolism results in the production of a number of waste materials (**excretions**), of which the CO_2 evolved during respiration is one. Now let us consider the supply and expenditure of **energy**: plants obtain energy in various ways; from the sun's heat (and in the case of green plants from the sun's light also), and from the organic food absorbed by such plants as fungi, which are incapable of making organic material for themselves. Whether, as in the latter case, the complex carbon-compounds taken in as food are absorbed ready-made, or, as in green plants, they are manufactured in the plant-cells, the substances so obtained represent so much **potential** energy which becomes converted into the **kinetic** (or active) form during the katabolic processes. Just as in our own bodies the energy which we exhibit as living beings and that keeps our bodies warm and enables us to move is the result of oxidation in the tissues by which CO_2, H_2O, and other substances are produced, and as in the burning or oxidation of coal the stored (potential) energy is liberated in the active (kinetic) form, so the similar but slower production of energy in plants, as shown in the production of heat, the slow but incessant movement of protoplasm in cells, the movements due to growth, irritability, &c., can go on only as long as the plant is supplied with the oxygen necessary to liberate the energy in the active or kinetic form.

That heat is developed in plants may be proved by experiment,

choice being made of material in which the katabolic processes are active, such as opening flower-buds or germinating seeds. A handful of dandelion heads is placed in a large funnel supported over a beaker partly filled with caustic potash solution, and a delicate thermometer is arranged with its bulb embedded in the flowers. A second funnel and thermometer are similarly arranged, but in this case damp sawdust is used instead of the flower-heads. The object of the damp sawdust is to equalize the conditions of the two thermometers and to prevent the one among the flowers acting as a wet-bulb. The whole should be covered with a large glass bell-jar supported a little below to allow the air to enter. The potash absorbs the CO_2 produced and so brings about change of air among the flowers. In an experiment it was found that the thermometer with its bulb among the flower-heads registered a temperature about 2° C. higher than the one in the sawdust.

Plants are not usually at a higher temperature than the surrounding air, because of the continual and rapid loss of heat which takes place by radiation and transpiration.

The Products of Metabolism.

We have already seen how, as a result of constructive metabolism, carbohydrates (sugar and starch) are formed in the green parts of plants, and that during the period of carbon-assimilation, i. e. in the daytime, the formation of carbohydrates may be so rapid as to be beyond the immediate necessities of the plant, and lead to the storage of starch by the chloroplastids.

The **chloroplastids** have various forms (Fig. 210): the most common one is that of rounded grains known as 'chlorophyll grains,' or 'corpuscles,' which multiply by division, and is the only form represented in the higher plants: the greatest divergence of form is found in the algæ, where they may be small rounded bodies (e. g. *Vaucheria*, *Bryopsis*, Fig. 210, VI), starlike (e. g. *Zygnema*, Fig. 210, V), flattened and ribbon-like (e. g. *Spirogyra*, Fig. 140, p. 246), &c.

A chloroplastid, whatever its shape may be, always consists of two parts: (1) the *protoplasmic basis*, which is of the same shape and size as the chloroplast itself, and (2) the *chlorophyll*, which appears to exist as a solution permeating the substance of the colourless plastid. It is the protoplasmic basis which does the work of assimilation and starch-formation, not the chlorophyll itself; the latter merely serves as an intermediary between the source of the energy (i. e. sunlight) by which the work is done and the protoplasm which makes use of

the energy to do the work (see p. 416). Chlorophyll is soluble in alcohol, and so is dissolved out when green leaves, &c., are kept in methylated spirit, leaving nearly colourless grains behind. But the starch which is stored in leaves and other parts during sunlight disappears as such if the plant is kept for a time in darkness, or even to a great extent under natural conditions during the night. We have already pointed out that it is reconverted into sugar by the agency of an enzyme known as diastase, which is formed by the protoplasm and

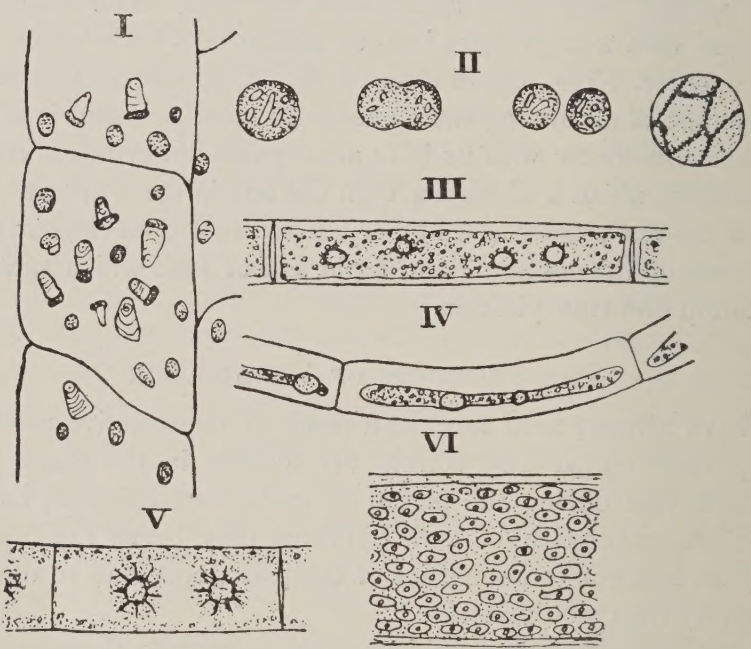


FIG. 210. Chloroplastids. I. Some cells from the stem of *Pellionia*, showing chloroplasts (small dark bodies) and starch grains (oval, lighter bodies). II. Chloroplasts of a Moss, showing stages in division and included starch grains. The grain at the extreme right is an old one and is made up almost entirely of starch. III. A cell of *Mougeotia* (a green Alga), showing the flat chloroplast with a row of pyrenoids. IV. The same in a strong light. The chloroplast is now seen on edge. V. A cell of *Zygnema* (an Alga closely related to *Spirogyra*), showing the two star-shaped chlorophyll bodies, each with a central pyrenoid. VI. Part of a filament of *Bryopsis* (another Alga) with very numerous small chloroplasts, each with a single central pyrenoid.

about which more will be said later (p. 452). The soluble carbohydrate which is thus produced passes out of the assimilating organs to other parts; some of it is at once used by the protoplasm at the growing points, for the production of new cell-walls, &c., and the rest is again stored in some of the more deeply seated cells until required. Carbohydrates are commonly stored as reserve food-material in seeds, tubers and other underground stems, bulbs, corms, tap-roots, &c. If we cut sections of the cotyledons of the seed of the pea (Fig. 215, IV, s),

the cells will be found to contain large starch grains ready to be used as food-material for the young plant before the development of leaves enables it to provide for itself.

If we cut sections of the stem-tuber of the potato, we shall find that the cells are packed with starch grains (Fig. 211, III, IV, V, VI), representing so much food-material for the young plants which will grow from the buds or 'eyes' upon its surface. The rhizome of Solomon's seal is a similar storehouse, as is also the root-tuber (a

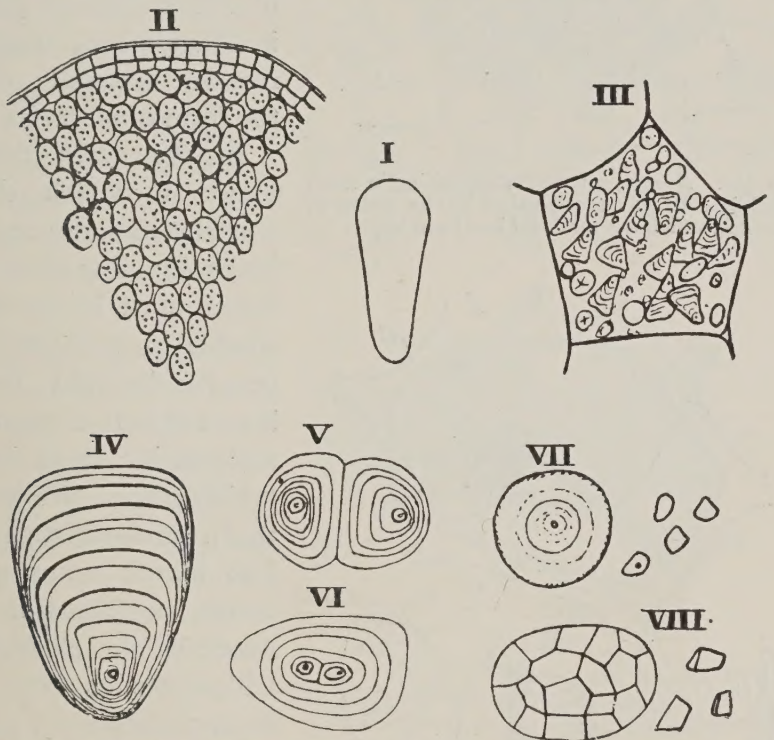


FIG. 211. Starch grains. I. Root-tuber of the Lesser Celandine. II. The same in section, showing parenchymatous cells filled with starch grains (represented by dots). III. Cell from a tuber of the Potato, showing starch grains. IV. A starch grain of the Potato. V. Compound grain of the Potato. VI. Half compound grain of the Potato. VII. Starch grains of Wheat. VIII. Starch grains of Oat. The large grain is a compound grain, the smaller ones are the isolated component grains.

swollen root, not a stem) of the lesser celandine (*Ranunculus Ficaria*, Fig. 211, I, II). Carbohydrate may be stored in forms other than starch: cut sections of a date-stone, and note the very thick cellulose cell-walls (Fig. 222, p. 462), showing that the reserve material has been laid on the original thin walls instead of being stored in the form of starch grains. Sugar is stored, dissolved in the cell-sap, in the sugar-cane, in the fleshy leaves of the bulb of the onion, and in the thick fleshy root of the beet.

If we examine sections of the tuberous roots of the dahlia which have been kept in spirit, we shall see peculiar crystallized bodies (**sphærocrystals**), due to the precipitation by the spirit of the carbohydrate **inulin** which was formerly in solution in the cell-sap (Fig. 212).

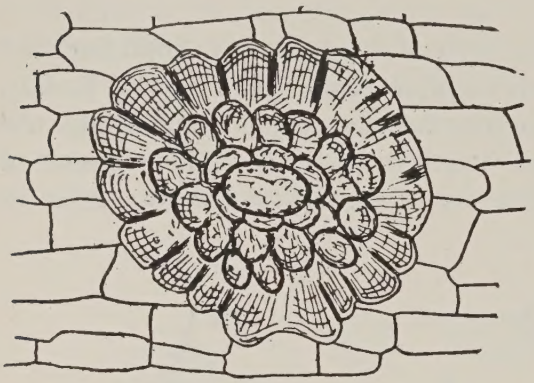


FIG. 212. A large sphærocrystal of inulin from the Dahlia tuber, as precipitated by the action of the spirit in which the material has been kept.

Sometimes, as in the seeds of the castor-oil plant and in the almond, some of the reserve material occurs in the form of oil or fat.

In the cases mentioned above in which starch is stored in underground tubers, bulbs, &c., it is clear that the starch must be formed from soluble carbohydrate (i. e. sugar), brought from the leaves and other organs where assimilation is, or has been, taking place. We have seen that a similar change of sugar into starch takes place in leaves, and that it is brought about by the chloroplastids. Chloroplastids are absent from underground parts, but their place as 'starch-formers' is taken by the **leucoplastids**, which only differ from chloroplastids in the absence of the green colouring material. Fig. 213, II, shows some of these leucoplastids with their associated starch grains from the tuber of an orchid; it will be noticed that the starch grains are of different relative sizes, and that more than one grain may be formed by a single leucoplast. Leucoplasts

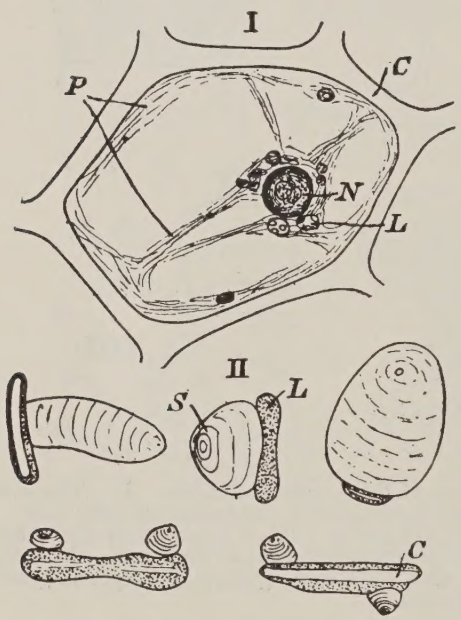


FIG. 213. Leucoplastids, &c. I. A cell of *Tradescantia*, showing leucoplasts aggregated around the nucleus. The leucoplasts contain highly refractive starch grains. C = cell-wall; L = leucoplasts; N = nucleus; P = protoplasm with strands passing to the nucleus. II. Leucoplasts and associated starch grains from the tuber of an orchid. L = leucoplast; S = starch grain. The leucoplast contains a rod-like proteid crystalloid (c).

may also be seen by examining sections from very young potato-tubers, and in fact from almost any tissue in which storage of starch is taking place. If a potato-tuber is partly uncovered and exposed to light it becomes green in colour, owing to the development of chlorophyll in the leucoplastids, which are then called chloroplastids. Both chloroplastids and leucoplastids may be called 'starch-formers,' but there is this important difference between them: a leucoplast is only able to make starch from sugar when the latter is supplied to it ready-made; whereas a chloroplast (in daylight) is not only able to change one form of carbohydrate (sugar) into another (starch), but is able to make the sugar itself from carbon-dioxide and water.

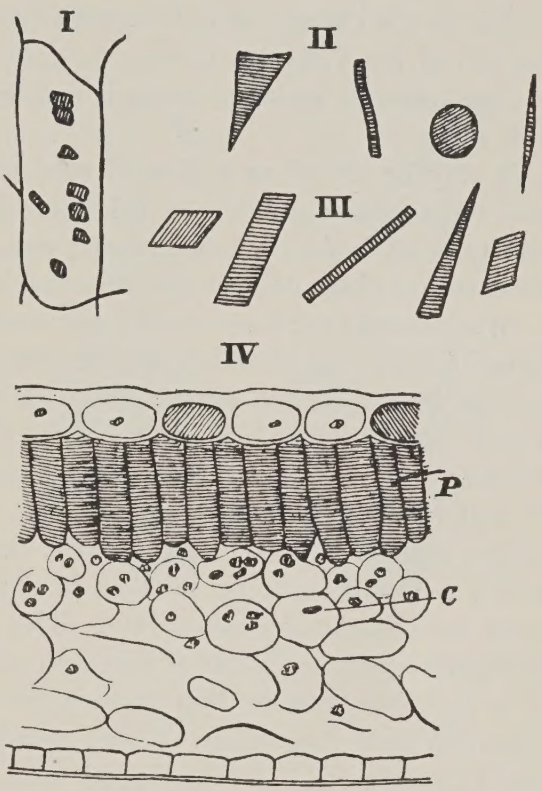


FIG. 214. Chromoplastids, &c. I. A cell from a sepal of *Tropæolum* containing yellow chromoplasts, to which the general colouration is due. II. Chromoplasts from the fruit of the Rose. III. Chromoplasts from the root of the Carrot. IV. Vertical section through a leaf of Virginian Creeper in the autumn. The palisade cells (P) and some epidermal cells contain red cell-sap. C = cells of spongy parenchyma with disorganized chloroplasts.

There is yet another kind of plastid to which reference may conveniently be made here, viz. the **chromoplastids**, which are closely related to the chloroplastids and leucoplastids. These are plastids which possess colouring matter other than chlorophyll. They are commonly formed by the alteration of chloroplastids whereby the plastid changes its shape and becomes yellow or orange in colour. Examine sections cut from the unripe 'hip' of the rose, and grains will be found in all stages of transition from chloroplasts to chromoplasts; the grains become yellow and then orange, at the same time becoming angular in outline owing to the formation of crystals within. Good chromoplasts may also be seen in the cells of the calyx in *Tropæolum* (the

so-called 'nasturtium' of gardens); it will be found that the general orange colouration is due to chromoplasts, but that where red lines occur the colour is due, not to solid bodies in the cells, but to coloured cell-sap. The root of the carrot is also good material in which to see orange chromoplasts. The colour of the leaves of the copper beech is due to the combination of red cell-sap with the green of the chlorophyll-bodies. The yellow colour of some leaves in autumn (e.g. poplar) is due to the change of chloroplasts into yellow chromoplasts, while the leaf of the Virginian creeper owes its beautiful autumn colouration to rose-coloured cell-sap, which is mainly in the palisade tissue (Fig. 214, IV).

It may be stated as a general rule (to which there are exceptions) that most yellow and orange colourations in flowers, leaves, &c., are due to solid bodies (chromoplasts) contained in the cells, and that most red and blue colours are produced by coloured cell-sap.

In addition to the above-mentioned reserve food-materials, viz. starch, sugar, fat, &c., all of which consist chemically of but three elements, carbon, hydrogen, and oxygen, there are other products of metabolism which contain, in addition to the three elements mentioned, nitrogen, sulphur, and phosphorus. Protoplasm itself is of similar composition, so that in the formation of new cells at the growing points and elsewhere, and as a consequence of the continual waste of protoplasm which is going on, fresh supplies of the nitrogenous food-substances must be constantly forthcoming. The details of the production of nitrogenous organic material by green plants are not well known, but it is probable that the first materials to be formed from the nitrates absorbed from the soil are of the nature of **amides** (such as **leucin** and **tyrosin**), and that light takes some part in this process, just as it does in the production of non-nitrogenous organic material. It is further supposed that from the amides the far more complex proteids are gradually formed in the companion cells of the phloem. However this may be, the excess of proteid is stored in seeds and other organs much in the same way as the carbohydrates are; in fact, everything is stored in a seed that is necessary for the young plant's early development.

Grains of proteid are known as **aleurone grains** (Fig. 215): many, such as those contained in the seeds of the pea and lupin, are very small and show but little structure (Fig. 215, IV, V), but the comparatively large grains found in oily seeds, such as those of the castor-oil plant (*Ricinus*, Fig. 215, I, II, III), show more complexity in structure.

Cut sections of the cotyledons of *Ricinus* and mount them in olive oil; the aleurone grains will be seen somewhat as shown in Fig. 215, I, each containing near one end a rounded mineral body, known as a **globoid**, and consisting chemically of a double phosphate of lime and magnesia. Now mount other sections in water; the grains will be observed as before, but one (sometimes more) proteid **crystalloid** may be seen which, with the globoid, is embedded in the proteid matrix of the grain. Sections should also be cut from the cotyledons of the pea and lupin for comparison with *Ricinus*.

It may be well to indicate the chemical relationship of the various reserve materials in the form of a table:—

A. Non-nitrogenous; consisting of carbon, hydrogen, and oxygen only.

I. **Carbohydrates.** With the H and O in the same proportion as in water, H_2O. This division includes three groups of bodies:

i. *The starch group* with the empirical formula $C_6H_{10}O_5$. This group includes starch, cellulose, inulin, &c.

ii. *The cane-sugar group* with formula $C_{12}H_{22}O_{11}$. This group includes cane-sugar and maltose.

iii. *The grape-sugar group* with the formula $C_6H_{12}O_6$. Includes grape-sugar, dextrose, &c.

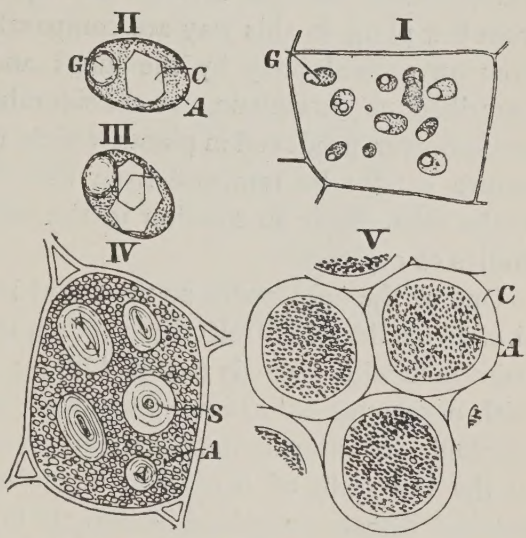


FIG. 215. Protei* or aleurone grains. I. A cell of the endosperm of *Ricinus* examined in oil, showing some of the aleurone grains. G=globoid. II. A single aleurone grain of *Ricinus* in water. A=amorphous proteid, in which the globoid and crystalloid are embedded; C=crystalloid; G=globoid. III. An aleurone grain containing two crystalloids. IV. A cell from one of the cotyledons of the Pea, showing large starch grains (S) and small proteid grains (A). V. Cells from a cotyledon of the lupin. The cells are filled with small proteid grains (A). The carbohydrate reserve is in the form of cellulose in the thick cell-walls (C).

II. **Fats and Oils.** These differ from the carbohydrates in containing relatively less oxygen, i. e. not sufficient to fully oxidize the hydrogen present.

B. Nitrogenous; consisting of carbon, hydrogen, oxygen and nitrogen, with, in the proteids, sulphur and phosphorus.

I. *Amides.* Soluble in water and diffusible. *Ex.* asparagin, leucin, &c.

II. *Proteids.* Much more complex than the amides and indiffusible. *Ex.* albumose, globulin, &c.

Waste Materials. In the metabolism of plants a number of waste products are formed, just as in our own bodies the waste materials, water, carbon-dioxide, and urea, are produced. Of the waste products produced by plants, some, such as water, the oxygen liberated in connexion with carbon-assimilation, and the carbon-dioxide produced in respiration, are removed from the plant in the gaseous form and pass into the atmosphere. The substances removed from the plant in this way are comparable to the substances removed from an animal body by the lungs and skin, and may be similarly described as excretions. A considerable number of waste materials are, however, produced in plants, which, on account of their non-volatile nature, cannot be removed from the plant, and so are found stored in the cells, either in solution in the cell-sap or separated out as solid bodies or crystals.

One of the substances so produced is **oxalic acid**; this occurs free (i. e. as oxalic acid itself) dissolved in the cell-sap, and is important in connexion with osmosis (see p. 429); a great part, however, combines with a mineral base (lime) and forms **calcium oxalate**, which, being insoluble in water, is deposited as crystals in the cells. Cut sections of the leaf-stalk of *Bignonia*, and observe the clustered crystals of calcium oxalate contained in many of the cells. Some cells may contain single crystals and their shape can then be made out. Similar crystals may be seen in the leaf of the beech. The composition of the crystals may be tested for in the following way: irrigate the section with acetic acid, and notice that the crystals are not affected nor does gas escape, proving that the crystals do not consist of carbonate of lime; next irrigate with sulphuric acid (50 per cent.), and see that the crystals are dissolved. New crystals may appear which are composed of calcium sulphate and are produced by the action of the sulphuric acid.

In many plants, especially monocotyledons, crystals of calcium oxalate of a different form are deposited; these are long needle-like crystals arranged in bundles and known as **raphides**. They are well seen in the membranous scales which surround the bulb of the Roman hyacinth, also in the similar scales of the onion and in sections of the leaf of *Agave*. Each bundle of crystals will be found to be contained in a specially large cell known as a **crystal-sac**, showing that in this case the crystals were deposited at the same time as the tissue

was formed, and not by subsequent precipitation. On the other hand, the single and cluster crystals are found deposited in ordinary cells, and are generally deposited long after the cells are first formed. An interesting case is seen in the deposition of this waste material—calcium oxalate—in the cells of deciduous leaves (see Fig. 216), so that in the autumn a tree gets rid of a considerable amount of useless material in this way.

Another waste product is **calcium carbonate.** This may be de-

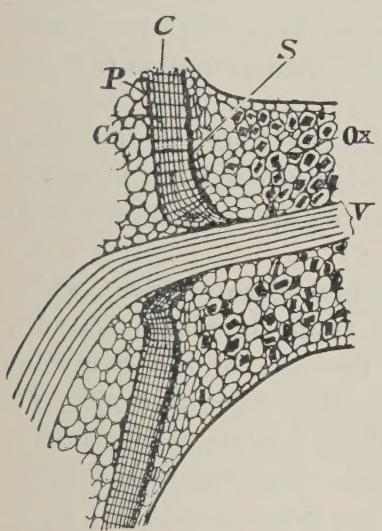


FIG. 216. Vertical section through the base of petiole of Horse-chestnut in autumn to illustrate the cause of the fall of the leaf. The fall of the leaf is due to the formation of a definite separating layer (S). C = cork; CO = cortex of stem; OX = crystals of calcium oxalate in leaf; P = phellogen; V = one of the vascular bundles of the leaf.

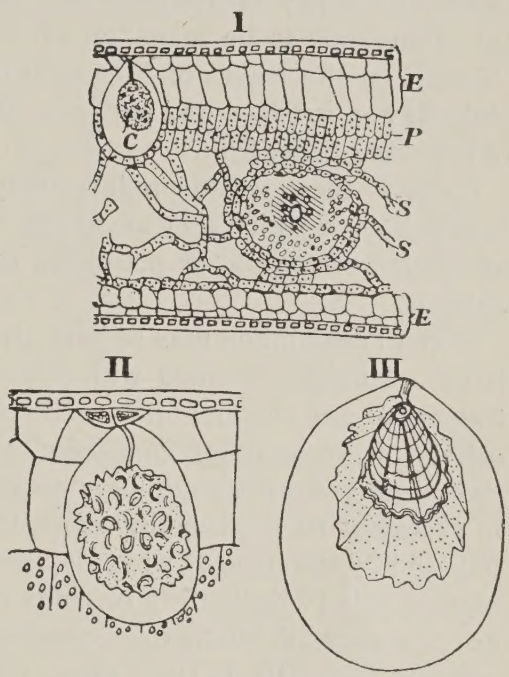


FIG. 217. Cystoliths in *Ficus elastica*. I. Vertical section of leaf. C = cystolith; E = many-layered epidermis; P = palisade mesophyll; S = spongy mesophyll. II. Cystolith and surrounding cells more highly magnified. III. The cellulose basis of a cystolith left after solution of the carbonate of lime in acid.

posited as granules or crystals in the cells; or deposited in the cell-walls (as in calcareous algæ); or it may be excreted in solution by special glands (**chalk glands**) associated with water stomata (Fig. 207, p. 436). A peculiar mode of deposition of carbonate of lime is seen in the **cystoliths** of *Ficus elastica* (Fig. 217). Vertical sections of the leaf should be cut; notice the many-layered epidermis on both surfaces of the leaf which serves as a **water-reservoir tissue**; in some specially large epidermal cells the cystoliths will be seen, each consisting of a globular calcareous body suspended by a stalk. Treat the section

with acetic acid, and the outer calcareous part of the body will dissolve with evolution of CO_2, leaving a basis of cellulose showing radiating and concentric structure, and which is really an ingrowth of the cell-wall above.

Another common waste product is **tannin**, which occurs in many plants, often contained in special cells with cuticularized walls called **tannin-sacs**. **Resin** may also occur in cells. The layer of **wax** which forms the 'bloom' on some ripe fruits and leaves, may be mentioned here; in the plum and cherry the 'bloom' is seen under the microscope to be made up of fine granules of wax; the white 'bloom' on the leaves of *Eucalyptus globulus* is caused by a layer of globular and rod-like wax particles, as is also the covering of the stem of the sugar-cane, &c.

Some of these waste products may be of some use to the plants in which or on which they are found. Wax is a protection against wet, and bitter, astringent, or poisonous substances are a protection from animals.

A short description may be here given of **laticiferous tissue**, which, if not entirely concerned with waste materials, is mainly so. Cut transverse and longitudinal sections of the root of the dandelion, salsafy, or some other composite with a milky juice (**latex**). The central part of the fleshy root is occupied by the xylem, which here (as in succulent roots generally) consists largely of parenchyma; this is followed by the phloem, which is also mainly parenchymatous. In the phloem will be seen rows or rings of cells with dark contents, which are the ends of laticiferous vessels, as is well seen in longitudinal sections (Fig. 218, I, II). These vessels, which anastomose with one another so as to form a network, are formed by the solution of the cross-walls of a number of transverse and longitudinal rows of cells.

Similar laticiferous vessels may be found in the poppy and in the *Campanulaceæ*. In the greater celandine (*Chelidonium majus*), one of the *Papaveraceæ*, the latex may be seen as an orange-red fluid which exudes from any broken surface; in this case also the latex is contained in vessels, but there are no cross branches between the longitudinal rows of cells, i. e. the vessels are not connected up into one system of anastomosing tubes as in the plants above mentioned.

In the spurges (*Euphorbia*) and some other plants a different arrangement is seen: laticiferous *cells* are present in the embryo, and these grow and increase in length with the growth of the plant in which they are contained. In transverse and tangential sections of

the stem of *Euphorbia splendens* or other species, there may be seen in the cortex the thick-walled latex 'cells,' which in longitudinal sections appear as long tubes – they branch but never anastomose, and there is no indication of cross-walls such as are seen in some laticiferous vessels. These so-called 'laticiferous cells' are really *cœnocytes*, as they possess a number of nuclei. The cell-walls of laticiferous tissues are always composed of cellulose and may be either thick or thin. The contents are very varied: besides the protoplasmic lining with its nuclei the granular contents of the vessels or cœnocytes contain many waste materials, such as **alkaloids** (the opium of the poppy is one of these), **oils, resins, caoutchouc, gutta-percha**, &c. In addition to these, food-substances may be present, e. g. large dumb-bell shaped starch grains in the cœnocytes of *Euphorbia* (Fig. 218, IV).

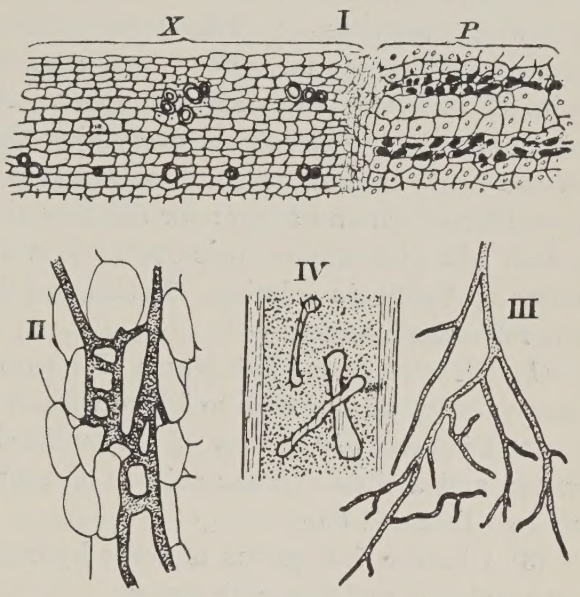


FIG. 218. Laticiferous tissue. I. Transverse section of part of the root of the Salsafy (*Tragopogon*), one of the Compositæ. X = the xylem typical of a fleshy root, consisting of much parenchyma with isolated groups of vessels; P = the phloem with transverse sections of many of the anastomosing laticiferous vessels with stained contents. The phloem consists mainly of parenchyma. II. Longitudinal radial section through the phloem of salsafy, showing anastomosing laticiferous vessels. III. A portion of a laticiferous cell or coenocyte of *Euphorbia*. IV. A portion of the same on a larger scale, showing the thick walls, granular contents, and peculiar starch grains.

The Work of Enzymes and Fermentation.

It has been already pointed out that in seeds and tubers, where carbohydrate in the insoluble form of starch is commonly stored, as well as in leaves and other parts of plants, a substance is formed by the protoplasm of the cells which is capable of changing insoluble starch into soluble and diffusible sugar, i. e. into a form which is capable of diffusing through the plant to the places where it is required.

This substance is known as **diastase**, and it is a representative of a large class of bodies, called **enzymes**, which play a very important part in both animal and plant economy. The change which takes place during the germination of a starchy seed may be demonstrated by the following experiments :— Take some ordinary barley-grains and crush them well in a mortar, after which they should be boiled for a few minutes in a small quantity of water. A little of the solution so obtained (which will contain everything that exists in a soluble form in the cells, as well as substances soluble in boiling water) is now tested for starch and sugar; for the former by adding iodine solution, which will give a blue colouration if starch is present, and for the latter by Fehling's solution. Fehling's solution is made and used in the following manner :—

(1) Dissolve about 104 grams of pure copper (cupric) sulphate in warm water and make up to 1 litre with distilled water.

(2) Dissolve 320 grams of crystallized potassic-sodic-tartrate in water, add a little carbolic acid to prevent the growth of fungi, make up to 1 litre and filter.

(3) Dissolve 150 grams of sodic hydrate in water, decant or filter and make up to 1 litre with water.

Fehling's solution should be made as required by mixing (1), (2), and (3) in equal quantities. To test for sugar (dextrose or maltose), a little Fehling's solution is added and the mixture boiled; if either of the above sugars is present a yellow precipitate of cuprous hydroxide, followed by red cuprous oxide, appears, owing to the reducing action of the sugar.

In the experiment with the extract from ungerminated barley-grains abundance of starch will be found, but no sugar. If now some of the grains are allowed to germinate in moist sawdust or sand, and the extract again tested for starch and sugar (care being taken to well pound the grains in a small quantity of water), both will be found present, owing to the action of the diastase having converted some of the starch into the form of sugar known as maltose, so called because it is the sugar formed in the process of malting. In the operation of malting, barley-grains are made to germinate by moisture and heat, and afterwards dried to prevent further action, the sweet-tasting dried material constituting malt. Another interesting experiment is to make a solution of diastase by crushing some malt in a small quantity of water, or by pounding some sprouting barley-plants, and adding a small quantity of weak starch solution (about

·2 gram of dry starch in 200 cc. of boiling water): a little of the mixture should be at once tested with iodine, and again after an interval of a couple of hours or more, when it will probably be found that the starch has all disappeared. The final product of the action of diastase on starch is **maltose**, one of the cane-sugar group of carbohydrates (see p. 447), but at the beginning of the action two intermediate products are formed, **dextrin** and **amylodextrin.**

Diastase, like all other enzymes, is produced by the protoplasm of the cells, and it shows no tendency to diffuse through the cell-walls, so that normally its work must be done within the cells: but although this is the case the enzyme may be separated from the living cells, it may be precipitated by alcohol, filtered off and dried, and still retain its power, when dissolved in water, of changing starch into dextrine and maltose. It is clear, therefore, that although enzymes are formed by the protoplasm they act independently of it, and that the changes produced are chemical in nature and not vital, i.e. not dependent on the living activity of the protoplasm itself. Although enzymes are destroyed as such by a temperature above 80° C., they may be kept under conditions which would be fatal to life.

An interesting enzyme is that recently discovered by Buchner in the yeast-plant (*Saccharomyces*). This plant has already been described (p. 266), as far as its morphology is concerned: it remains now to discuss its activities from a physiological standpoint. It was discovered at an early period that the yeast-cell possesses the remarkable power of so changing the sugary solution in which it lives as to lead to the change of sugar into alcohol and carbon-dioxide gas, and it was believed until recently that this change, known as **alcoholic fermentation,** could only go on as long as the fermenting liquid contained living yeast-cells. Two classes of ferments were thus recognized: those, such as yeast, which required the presence of living protoplasm were distinguished as **organized ferments,** while others, such as diastase, which may be extracted from the cells and can produce their characteristic effects quite apart from protoplasm or cells, were called **unorganized ferments or enzymes.**

But the so-called organized ferments are being rapidly reduced in number by the discovery that extractable enzymes may be obtained from them. Within the last few years Buchner, Green, and others have shown that yeast will yield an extract which can set up alcoholic fermentation in a solution of cane-sugar in the complete absence of yeast-cells. The yeast is subjected to a pressure of 200–300 atmo-

spheres, and the solution obtained filtered under pressure through porcelain in a Berkefeld or Pasteur-Chamberland filter, in order to remove all traces of suspended matter. Such a solution contains the ferment or enzyme (known as **zymase**), and that its action is a purely chemical one is evidenced by the fact that it is active in the presence of antiseptics which are fatal to protoplasm. If a solution of grape-sugar is fermented by the enzyme in yeast the change may be represented by the following equation:—

$C_6H_{12}O_6$	=	$2C_2H_6O$	+	$2CO_2$
Grape-sugar	=	*Alcohol*	+	*Carbon dioxide.*

But the solution which is fermented during the brewing of beer does not contain a sugar with the formula given above, but maltose, which is one of the cane-sugar group, and has the formula $C_{12}H_{22}O_{11}$. The fermentation of cane-sugar or maltose really involves two distinct operations brought about by two enzymes: cane-sugar or maltose is incapable of undergoing alcoholic fermentation as such, and must first be converted into sugars of the formula $C_6H_{12}O_6$. An enzyme is present in malt which will do this: it is known as **maltase**, and causes the maltose to change into glucose or grape-sugar by the taking up of water, as represented in the following equation:—

$C_{12}H_{22}O_{11}$	+	H_2O	=	$2(C_6H_{12}O_6)$
Maltose	+	*Water*	=	*Glucose*

after which the zymase ferments the glucose according to the equation given above.

Similarly a solution of cane-sugar is changed by a ferment known as **invertase** (which may be extracted from yeast) into a mixture of two other sugars:—

$C_{12}H_{22}O_{11}$	+	H_2O	=	$C_6H_{12}O_6$	+	$C_6H_{12}O_6$
Cane-sugar	+	*Water*	=	*Glucose*	+	*Fructose.*

each of which then undergoes fermentation into alcohol and carbon-dioxide.

An experiment to illustrate alcoholic fermentation may be performed in the following way: Half fill a large glass flask with a solution of cane-sugar in ordinary water, or, better, a special culture solution, such as **Pasteur's fluid**, made by mixing the following:—

Potassium phosphate	10 grams.
Calcium phosphate	1 gram.
Magnesium sulphate	1 „
Ammonium tartrate	50 grams.

For use, 1 gram of this mixture is mixed with 12 grams of sugar and

the whole dissolved in 70 cc. of water; the flask is provided with a stopper and bent delivery-tube dipping into lime-water, and a little ordinary yeast is added to the culture fluid. After a short time, especially if the preparation is kept in a fairly warm place, gas will be seen to pass off into the lime-water and make it 'milky,' proving the presence of CO_2, and after the action has stopped, the fluid may be tested for sugar with Fehling's solution (p. 452), and for alcohol by distillation at a temperature of 80° C.

Small quantities of other substances are produced in alcoholic fermentation besides alcohol and CO_2, the most important being glycerine and succinic acid.

Yeast will live either in the presence or absence of oxygen. Experiments made by Pasteur show that in the absence of oxygen fermentation proceeds very slowly compared with the rate at which it takes place when oxygen is freely supplied, and that in the absence of oxygen the growth of the yeast-plant itself is a very wasteful process. In the presence of O, for one part of yeast formed only 4 to 10 parts of sugar are decomposed; while in its absence some 60 to 80 parts are used. These experiments show clearly that yeast thrives much better in the presence of oxygen than in its absence.

Other enzymes of importance besides diastase are brought into action during the germination of seeds in order to change the various reserve food-materials into soluble and diffusible forms. **Inulase** brings about the change of inulin (see p. 444) into sugar. **Cytase** similarly converts the cellulose of seeds, in which the carbohydrate is stored in that form, as in the date.

The proteid (aleurone) grains have also to be changed into soluble forms, and there are special enzymes which change them into **peptones** and **amides**, a similar action to that which is carried on in the animal economy by the pepsin and trypsin of the gastric and pancreatic juices.

During the germination of oily seeds the oil gradually disappears owing to its decomposition into glycerine and fatty acids by the action of certain ferments; from the products of this decomposition carbohydrates are formed, so that as the fat gradually disappears carbohydrates take its place.

To sum up: an enzyme is a substance which can be extracted from cells and which is capable of setting up chemical changes in certain media in which it may be placed, such change or decomposition generally involving the taking up of one or more molecules of water.

The most important enzymes present in plants may be classified thus :—

(i) Those which change insoluble carbohydrates into soluble and diffusible ones ; e. g. diastase, inulase, cytase, &c.

(ii) Those which change more complex sugars into less complex ones, e. g. invertase, which 'inverts' cane-sugar into grape-sugar.

(iii) Those which act on proteids and convert them into soluble and diffusible peptones and amides.

(iv) Those which decompose oils and fats.

(v) Alcohol-producing enzyme—zymase[1].

Transpiration.

This process, by which plants continually lose water, is one of very great importance, resulting, as it does, in conjunction with root-pressure, in the passage of a rapid current of water with substances in solution from the roots upwards to the leaves. Plants absorb their food in such very dilute solutions that a considerable amount of excess water must be got rid of, and it is lost mainly as vapour through the stomata of the leaves. The stomata open and close according to the turgidity of the guard-cells—the more turgid the latter, the larger are the pores ; as a rule the stomata open in the daytime and close at night, so that they are open when carbon-assimilation can go on, and the processes of transpiration and assimilation proceed together, the stomata serving both to admit gases into the leaf, and to allow water-vapour to pass out of it.

The influence of the turgidity of the guard-cells on the size of the pore may readily be observed by tearing off a piece of the epidermis of the iris or other plant, and plasmolysing the guard-cells with salt solution (see p. 434) ; as the cells lose their turgidity the pores close.

The rate at which transpiration takes place may be roughly ascertained by determining the rate at which water is absorbed, using the apparatus shown in Fig. 219. Take a large leafy branch, which should, if possible, be cut from the parent plant under water, and kept with its lower end immersed until required. The apparatus is set up as shown in the figure and filled with water, the lower end of the tube B being stopped with the finger while still under water. The

[1] For a full recent account of fermentation and enzymes see Prof. Green's *The Soluble Ferments and Fermentation*. Also an article in *Nature* (vol. 52) on 'Yeast and Alcoholic Fermentation.'

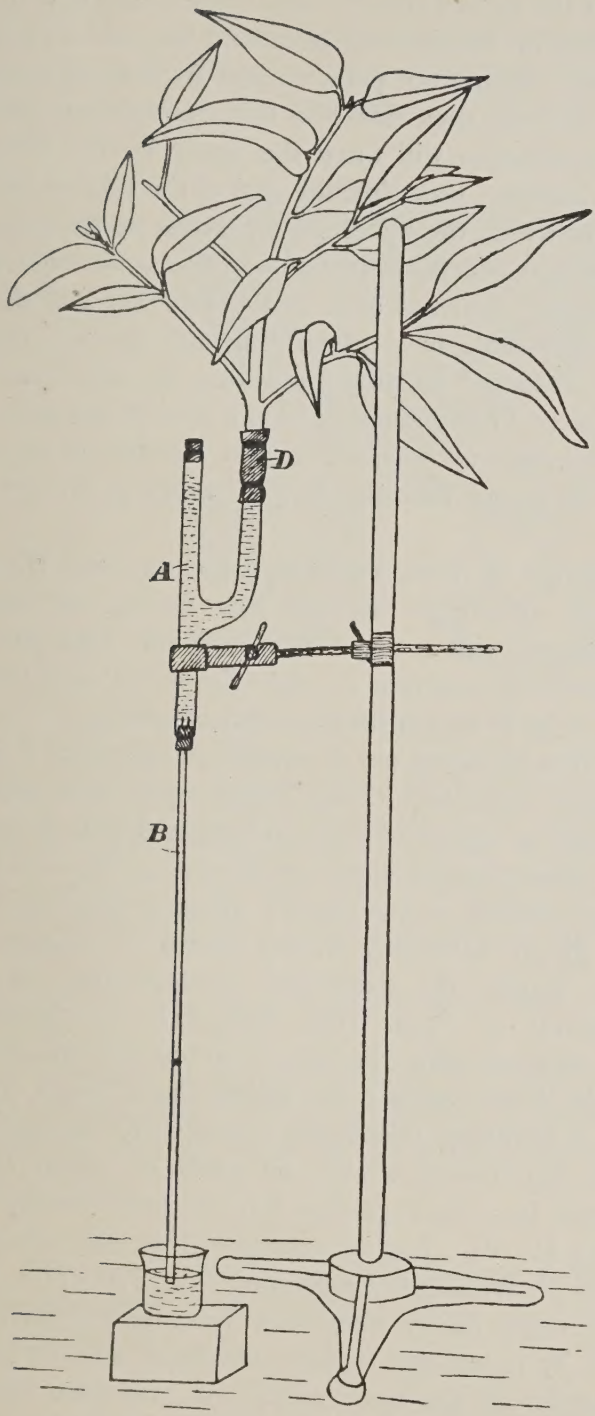


FIG. 219. Experiment to show the rate of absorption (and transpiration) by a leafy shoot. A = potometer completely filled with water; B = fine tube containing water and an air-bubble (black dot), connected with the potometer above and dipping into a vessel of water below; D = wired india-rubber connexion between the potometer and the leafy shoot.

branch is then forced into the rubber tube D, care being taken that no air is enclosed, and that the joint between the plant and the tube is well secured by tying with wire. Allow the plant to rest for a short time to get used to the new conditions, then raise the lower end of the tube (B) out of the water; transpiration will draw the water up the tube and air will enter at the bottom; now sink the end of the tube in the water again, and the rate at which the bubble of air moves up the tube affords an index to the rate at which absorption and transpiration are taking place. If the internal sectional area of the tube (B) and the length travelled by the air-bubble in a given time are known, the actual amount of water absorbed in that time may be calculated. To demonstrate the influence of the stomata on the rate of transpiration the surfaces of the leaves may be smeared with vaseline to close the pores, when it will be found that the loss of water is brought nearly to a standstill.

The withering of the leaves of some plants on a hot day, and their recovery at night, is due simply to the fact that during the day absorption has not kept pace with transpiration and the cells have consequently lost their turgidity, whereas at night the diminished loss of water has enabled the cells to regain their normal condition.

The rate of transpiration depends on a variety of factors: it is most active in a bright light, and other things being equal it is most active when the temperature of the air is high, and when the air is dry than when it is moist. Many plants show arrangements by which the loss of water by transpiration is restricted; these arrangements are especially found in plants belonging to dry places or climates, as would be expected. Notice the depressed stomata and thick cuticle on the needle-leaves of *Pinus* (Fig. 220, II); the 'rolled leaves' of the **Heath** (*Erica*) with the edges so curved inwards as to partly close in the lower surface on which the stomata are situated; and the **Ling** or **Heather** (*Calluna*), another dry moorland plant with its crowded four-rowed leaves, on each of which the stomata are not only sunk in a deep groove, but are protected by a number of hairs (Fig. 220, IV, V). A good example of the same thing is seen in the leaves of the **Crowberry** (*Empetrum*) (Fig. 220, I); here the leaf is rolled until the edges nearly meet, and even then the narrow cavity is nearly blocked by a number of close-set hairs, so that the stomata, which are situated on the inner epidermis, transpire their vapour into what is practically a closed cavity. In the **Oleander** the stomata occur only along the sides and bottom of a number of grooves,

and long hairs arise between them. Many moorland grasses (e.g. *Festuca*, &c.) also roll their leaves to restrict loss of water. Sometimes the stomata are protected by projections of the cuticle above them as shown in *Cypripedium* (Fig. 220, III). The leaves of succu-

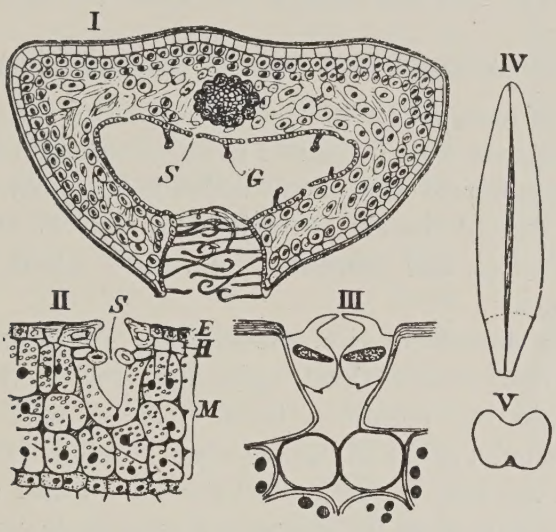


FIG. 220. Arrangements for restricting transpiration. I. Transverse section of leaf of Crowberry (*Empetrum*). The leaf is rolled, and where the edges nearly meet a number of interwoven hairs are developed. The stomata are confined to the closed-in epidermis, so that transpiration takes place into a closed cavity. G = glandular hairs; S = stomata. II. Part of transverse section of leaf of *Pinus*, showing the depressed stomata (S). E = epidermis with thick cuticle; H = hypodermis; M = cells of the mesophyll with infolded walls; the lowest layer of cells is the endodermis. III. One of the stomata, with adjacent cells, from the leaf of an Orchid (*Cypripedium*), showing the projections of the cuticle of the guard-cells above the pore. IV. Leaf of Ling (*Calluna*) seen from the under side, showing the groove in which the stomata are placed protected by hairs. V. Transverse section of same. The groove with hairs can be seen at the bottom of the section.

lent plants, such as cacti, aloes, &c., have very thick cuticles and lose water very slowly [1].

Those parts of plants which are covered with cork do not transpire, nor is water lost through the cuticle of ordinary leaves and stems; practically all the water lost by a plant escapes through the pores of the stomata.

[1] For a good account of the adaptations of moorland plants to restrict transpiration see an article by Prof. Miall, F.R.S., on 'A Yorkshire Moor' in *Nature*, vol. 58.

CHAPTER XXIV

THE MOVEMENTS OF PLANTS

Spontaneous Movements of Protoplasm.

The power of *spontaneous* movement is perhaps the most distinctive of all the characters which separate living protoplasm from non-living matter. This power of movement, which is popularly supposed to be exclusively an animal characteristic, is a property of protoplasm itself wherever it is found, and movement of various kinds may readily be studied in plants.

Spontaneous movement, i.e. movements which are not brought about by external stimuli (heat, light, moisture, &c.) but by causes operating within the organism itself, may be well studied in the streaming plasmodia of the **Myxomycetes**, a group of organisms which seem to lie on the very borderland of the animal and vegetable kingdoms. In one phase of its life-history a Myxomycete consists of a slimy mass of multi-nucleated naked protoplasm which crawls slowly about over the surface of rotting wood, decaying leaves, or whatever material it may be living upon, by putting out processes of its body (pseudopodia) in one direction and drawing them in in another, in the manner so well known in the common *amœba*. This amœboid movement is not, however, spontaneous nor does it go on at random: the direction of movement is distinctly a reaction to external stimuli, as is shown by the fact that, in its ordinary vegetative condition, the organism avoids dry and light places and moves to damper and less lighted spots. Moreover, after a time, when it is about to form its spores, its irritabilities entirely change in accordance with the conditions which are essential to spore-formation and dispersal, and it then seeks dry and light places.

But in addition to this induced amœboid movement which produces progression of the whole organism, the microscope shows that the internal protoplasm is in a constant rapid circulation or streaming, that is made evident by the movement of the granules contained in the protoplasm. In some cases the movement has been observed to go on for some little time in one direction, then to gradually slow up and start again in the opposite direction.

The Myxomycete gives us an example of protoplasmic movement,

both amœboid and streaming, in an organism which is untrammelled by the presence of a cell-wall, and it is similar to the movements shown by a large number of animal cells; but spontaneous movement of protoplasm is not, however, prevented by the presence of a cell-wall. Take a little of the common American water-weed (*Elodea*) and warm it in a water bath up to a temperature of about 30° C. (the protoplasm moves most rapidly when at about this temperature). Mount one of the leaves in water and examine the cell structure: the central part of the cell is occupied by a large vacuole, but this is surrounded by a lining of protoplasm with a nucleus and chlorophyll grains. The latter will be seen to be in motion up one side of the cell and down the other, being carried along in the moving protoplasm. This kind of motion is described as **rotation,** and may be seen in many plant-cells, and probably takes place in all. In addition to *Elodea* it may be well seen in the leaves of *Vallisneria spiralis*, a water-plant sometimes grown in aquaria, and in the root-hairs of aquatic and other plants.

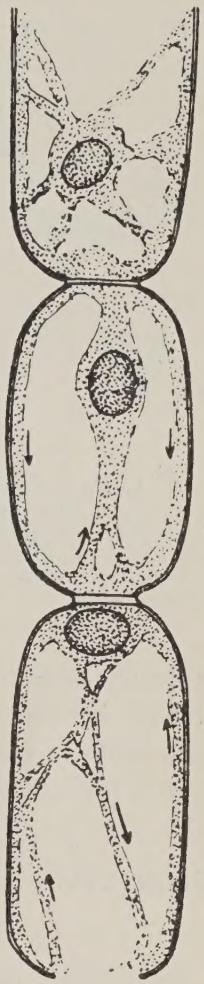


FIG. 221. Three cells from a staminal hair of *Tradescantia*, showing the circulation of the protoplasm. The arrows show the directions of movement.

A more complicated movement, but really of the same kind, may be studied in the flowers of *Tradescantia*, the spider-wort. Tear off a few of the coloured hairs from the base of a stamen and mount them in water: each hair will be seen to consist of a single row of somewhat barrel-shaped cells (Fig. 221). Each cell is lined with protoplasm, from which 'bridles' of protoplasm pass to the nucleus, which is generally situated somewhere near the centre of the cell; the greater part of the interior of the cell is filled with purple cell-sap. Focus some of the strands or 'bridles' of protoplasm and see the complicated movements of the granules and protoplasm. Currents may be seen to pass from the strands to the peripheral protoplasm and vice versa; sometimes currents in two directions can be seen in one strand. These complicated movements to and from the nucleus are usually described as the **Circulation** of the protoplasm.

It is possible that the protoplasm may even stream from cell to cell. The possibility of this is made clear when it is remembered that in a tissue composed of cells, the protoplasm of adjacent cells is in direct continuity. Fig. 222 shows parts of some of the cells of the endosperm of a palm; the unshaded portion represents the extremely thick cellulose walls, and the shaded portion the protoplasmic contents of the cells. A number of wide pits are shown, those of adjacent cells being opposite to one another and nearly meeting at the middle lamella; across the narrow connecting bridges are a number of very fine lines, which are really canals or pits, through which run fine protoplasmic threads uniting the cells. It thus appears that so far from a multicellular plant or member being a collection of separate units, it is really, in many cases at least, a continuous mass of protoplasm which is only *partially* divided by the cell-walls. Further reference will be made to '*the continuity of the protoplasm*' when dealing with the transmission of stimuli through the plant (pp. 473, 475).

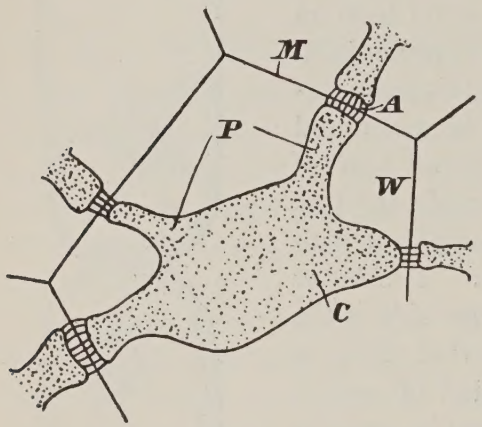


FIG. 222. A cell of the endosperm of palm, showing 'continuity of the Protoplasm' of adjacent cells. A = narrow pits carrying the connecting strands of protoplasm; C = cell cavity and contents; M = the middle lamella; P = wide simple pits; W = thick cellulose wall.

SPONTANEOUS MOVEMENTS DUE TO GROWTH, OR ACCOMPANYING GROWTH.

By growth is meant simply *change of external form* or *increase in size*; in most cases, though not in all, the increase in size which takes place as the cell, or as the plant, develops from the embryonic to the adult condition is accompanied by a change in external form. A spherical body such as that formed by the single cell of a yeast-plant, or by the many cells of *Volvox*, is the result of equal growth in all directions; a long filament such as that of *Vaucheria* or *Spirogyra* is the result of growth mainly in one direction (or in opposite directions along one line); in a fern-prothallium the growth takes place mainly in two directions, and results in the formation of a plate of cells;

in an ordinary higher plant, while growth takes place to a certain extent in all directions, that in one direction is much more vigorous than in the others, and so gives rise to the elongated form.

The rate of growth in length of a stem or flower-stalk may be determined in the following manner: Mark the stem at intervals of about ·5 cm., starting from the apex and continuing the marks backward for about two or three inches; also make a mark (with Indian ink) near the bottom of the stem, and measure the distance between this point and the apex. If possible the plant should be arranged so that it is illuminated from above only so as to prevent heliotropic curvature of the stem (see p. 469). Observe the plant after a few days and measure the distance between the fixed point and the apex; the increase in length will give the amount of growth during the period of observation. Examine also the marks made at equal distances behind the growing point: note that the distance between them has increased, showing that growth in length has taken place, and also that the marks are no longer at equal distances apart. The last observation is of importance because it shows that the growth is not uniform, i.e. that there is a distribution in the rate of growth behind the apex. It will probably be found that the lines drawn farthest from the apex are as near together, or almost so, as they were at first, and that the distance between the marks gradually increases in passing towards the apex up to a certain level and then diminishes again (unless too long an interval has elapsed between the observations), showing that the region of most rapid elongation is not at, but *behind*, the apex of the growing point. At the same time the fact that the marks situated but an inch or so behind the apex do not separate at all, clearly shows that the growth in length of the stem only takes place near its free end, i.e. that it is *localized* and *apical*.

A similar observation may be made with a growing root, which should be marked with lines 2 mm. apart, starting from the apex and continuing backward for about an inch (Fig. 223, III). Seedling beans or peas may be used when the roots are about two inches long: they should be suspended inside a wide glass bottle or bell-jar as shown in Fig. 223, I, and the atmosphere kept moist by placing some layers of wet blotting-paper or some water at the bottom of the jar, as shown in the figure.

It thus appears that in a growing stem or root three regions may be distinguished:—

(i.) The actual apex of the growing point where new cells are being

formed by cell-division. This is the *formative region*, and but little growth takes place here.

(ii.) A region situated at some distance behind the apex, where but little cell-division takes place, but the cells formed in the formative region rapidly increase in size, i. e. grow. This is the *region of elongation.*

(iii.) The region beyond the elongating one. Here the cells are fully formed.

It will of course be understood that each cell passes through the different regions successively—formed in the formative region, it grows to its full size in the region of elongation, and is finally left behind as a mature cell by the advancing growing apex.

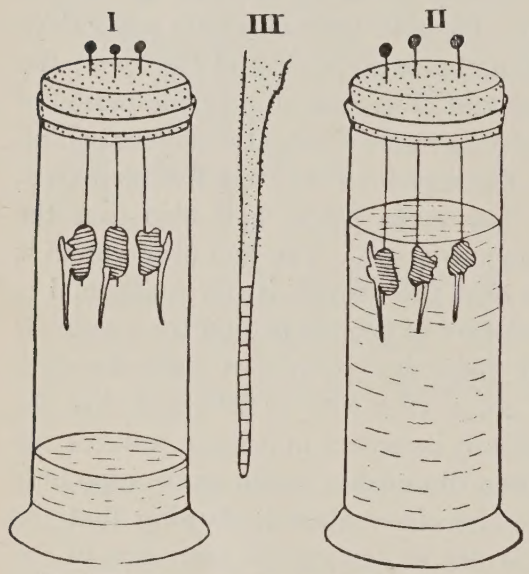


FIG. 223. An experiment on the localization of growth in length in roots and on the necessity of oxygen for normal growth. In I the impaled bean seedlings are growing in moist air over water. In II they are covered with water, so excluding oxygen. The growth in II will be much less than in I. III shows how to mark the end of the roots, as described in the text. The long pins in I and II pass through the cotyledons.

Besides the distribution in the rate of growth described in the preceding paragraphs there is also a variation in the rate of growth according to time. Any growing member, such as a stem or root, grows slowly at first and then goes on with increasing rapidity until a maximum rate is attained, after which the rate of growth gradually diminishes until it ceases altogether. This is known as the **grand period of growth**; it may be observed with seedling bean roots by making a mark on one of the cotyledons and measuring the length of the root from this fixed mark on successive days. A similar variation in the rate of growth is observable in the individual cell: its growth, at first slow, gradually increases to a maximum and then decreases, until growth in size ceases altogether and the cell is mature.

A growing member, such as an ordinary stem, does not constantly grow in the same direction, i. e. its direction of growth varies. Imagine a stem, the permanent or adult part of which rises vertically from the

soil: the actual growing region is not vertical but inclined, and moreover the direction of inclination undergoes progressive change towards all points of the compass. It will be understood that as the stem is also increasing in length its advancing apex, instead of growing upwards in a straight line, really describes a spiral path. This 'nodding' or **nutation** of the growing point is most easily observed in twining plants such as the hop, in which a complete revolution takes place in about two or three hours. The direction of nutation varies: in the hop and honeysuckle it takes place in the same direction as the hands of a watch go round, while the bindweed (*Convolvulus*) and bean (*Phaseolus*) nutate in the opposite direction. The former describe a left-handed spiral, and the latter a right-handed one. If a support is present these plants twine round it, and form either left- or right-handed coils according to the direction of nutation.

Normal growth can only take place as long as certain conditions are fulfilled:—

(i.) *A sufficiently high temperature is necessary.* An illustration of this is seen in the dormant condition of the trees in temperate climates during the winter, when not only are the growing points inactive, but the internal growing areas (the cambium, &c.) are in the same condition. Moreover a sufficiently high temperature is also necessary for the absorption of food by the roots and leaves, on which growth ultimately depends.

The most favourable temperature (or **optimum temperature**) varies somewhat with different plants and in different climates: in temperate climates it is generally between 25° C. and 30° C. (76° F.—86° F.). As the temperature sinks below this the activity of the functions gradually diminishes, and finally ceases altogether at a certain **minimum temperature**, which is usually a few degrees above the freezing-point of water; if the temperature rises above the optimum the same effects are produced. At a certain high temperature, generally about 50° C., the protoplasm is killed. A rough experiment to prove this can easily be performed: Cut a slice of red beetroot and wash it in water to remove the cell-sap liberated from the cells by the razor. Suspend it in a beaker of water which also contains a thermometer. Gradually raise the temperature of the water, and note the temperature at which the coloured cell-sap begins to escape into the water. As long as the protoplasm is alive the cell-sap does not escape, but when it is killed it at once begins to ooze out.

(ii.) *Air* (*oxygen*) *is necessary.* This may be shown by performing

an experiment similar to that figured in Fig. 223, I, II. Bean seedlings may be used, and a number should be selected having roots about equal in length. Some of these are grown in moist air as shown in the figure (I), and others arranged so that the roots and cotyledons are immersed in water so as to exclude the air (II); the water should be boiled previously to drive off atmospheric gases. After a day or two the roots may be compared; those kept in water will be found to have grown much less than those in air.

(iii.) *The cells of the growing points must be turgid* (see p. 433).

(iv.) Normal growth only takes place when the plant is supplied with all the necessary elements of its food, as can be demonstrated by water-culture experiments (p. 410).

Movements due to Chemical Stimuli (Chemiotaxis).

These movements have been already mentioned in connexion with the fertilization of the moss and fern (pp. 210 and 222), and the subject is of great interest and importance. The mucilage extruded from the female organ into the water in which fertilization takes place contains certain chemical bodies, malic acid in the case of ferns, and cane-sugar in that of mosses, by which the antherozoids are attracted to the archegonia. If a very fine glass tube containing malic acid or sodium malate is introduced into water containing fern antherozoids, the latter are at once attracted to the open end of the tube.

The Influence of Light on the Movements of Plants.

Variation in the intensity of the light often causes changes in the position of plant members as a whole, or of the contents of the cells. An example of the latter effect may be seen in *Elodea:* in dull light the chlorophyll grains of a leaf will be seen to be scattered through the lining protoplasm of the cells, and many will be seen on the upper and lower surfaces of the cells, i. e. on the surfaces which are most exposed to the light. If now the leaf is exposed to a bright light for some time, and again examined, the chlorophyll grains will be seen to have been carried by the protoplasm to the vertical walls of the cells and to present their edges (not their flattened surfaces) to the light. The physiological advantage of this movement would seem to be that, since light of great intensity leads to the decomposition of chlorophyll, the chlorophyll grains are protected in the manner described. Many

other leaves show the same phenomena, and with the change in position of the chlorophyll grains there is a change in colour of the leaf; indeed, most green leaves are paler in colour on a bright sunny day than they are in dull weather.

The influence of light on growth is very marked indeed. The general result may be expressed by saying that *light exercises a retarding influence on the growth of elongating organs.* Compare for example two potatoes, one allowed to sprout in a bright light and the other in darkness; the growth of the shoots of the latter will be very much greater than that of the former, the internodes of which will hardly grow at all. A plant grown in the dark will show other peculiarities besides the characteristic elongation of the internodes: it will have *small* leaves, and no chlorophyll will be developed, but only a yellow material called **etiolin** (hence plants grown in darkness are described as etiolated), &c.

If a potato tuber is allowed to germinate in a yellow or red light, by using a double bell-jar as shown in Fig. 197 (p. 414), the same effects are produced as by growing it in darkness, so far as the elongation of the internodes is concerned, showing that the retarding influence of light is produced by the more refrangible (blue) end of the spectrum.

It follows from the foregoing that we should expect a plant to grow more rapidly at night than during the day, and this is actually the case, but the actual amount of growth is largely modified by the other conditions, and particularly by variation in temperature: the lower temperature at night may be sufficient to prevent growth altogether.

The influence of variation in the intensity of light is also seen in the so-called sleep movements of some plants. An example is seen in the flower of the tobacco-plant (*Nicotiana*), which becomes widely open at dusk, and another example is seen in the daisy, which, however, closes in darkness. The trifoliate leaves of wood-sorrel (*Oxalis*), and of clover (*Trifolium*), also illustrate the same phenomenon; in both these plants the leaflets fold and fall downward so as to take a nearly vertical position at night with their edges directed to the sky. The bean (*Phaseolus*) also exhibits movements of its leaflets, and a short account may be here given of the mechanism of such movements. The leaf is articulated to the stem, and the leaflets to the rhachis, by cushions of tissue known as **pulvini** (Fig. 224, P, P′), on which the movements depend. A transverse section of a pulvinus (Fig. 224, III) shows that it consists mainly of parenchymatous tissue with thin walls: as long as the cells remain turgid (p. 433), the leaf

or leaflets are supported in their day position, but loss of turgidity of the pulvini at night leads to the drooping of the leaf into its night position. Most cases of movement in mature members depend on variation in the size of the cells, and in the turgidity of the tissues, of some portion of the motile organ.

In some cases (e. g. *Marsilea*, a vascular cryptogam), the leaflets

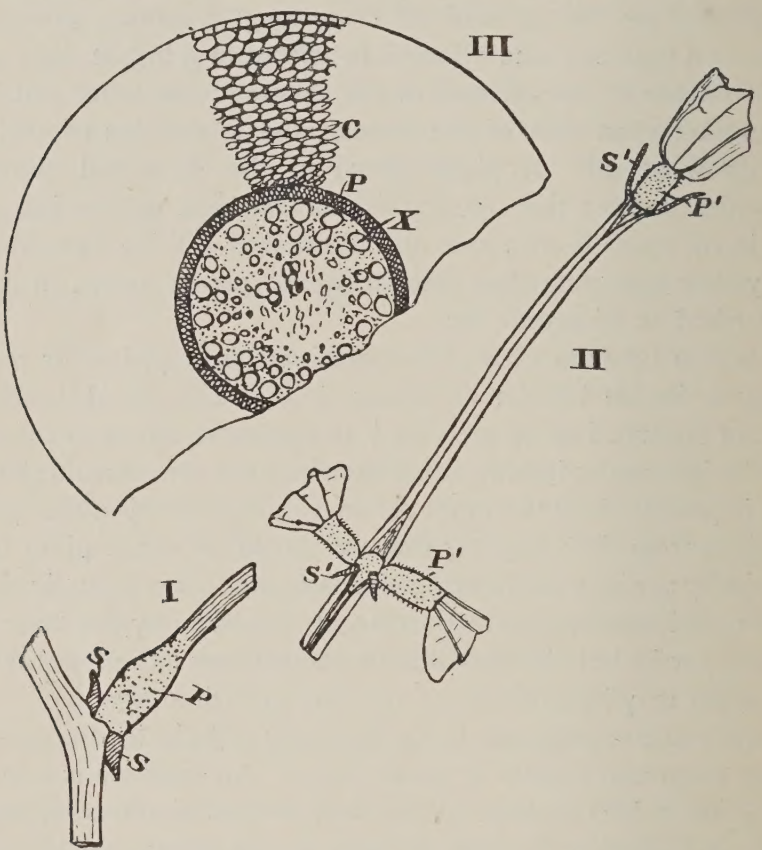


FIG. 224. Leaf of the Bean-plant (*Phaseolus multiflorus*), showing the pulvini, the cells of which lose their turgidity and allow the leaf and leaflets to droop into the night position. I. Stem and base of petiole. P = pulvinus at base of petiole; S, S = stipules. II. Distal part of a leaf seen from the under side. The leaflets have been cut short. P′, P′ = pulvini of the leaflets; S′, S′ = secondary stipules (stipellæ) at the bases of the leaflets. III. Diagrammatic transverse section of a pulvinus, showing the thick parenchymatous cortex (c), on the turgidity of the cells of which the position of the leaflets depends. P = phloem; X = xylem.

move upwards instead of downwards as in the clover, but in all cases the effect is to protect the leaves from injury by cold owing to excessive radiation of heat, as the leaf area which is exposed to the sky is reduced.

The growing leaves and cotyledons of many plants (e. g. cabbage) show movements due to variation in the intensity of the light. That

these movements are really due to this cause, and not merely to variation in temperature, is shown by the fact that they may be induced in the daytime: if a plant of clover is covered over so as to exclude all light, the leaflets will assume the night position in about an hour.

All the above-described movements which are due to variation in the *intensity* of the light are included in what is known as the **paratonic effect of light.** The rays at the blue end of the spectrum are the most active ones in this respect.

Some growing members, such as flattened foliage leaves with dorsiventral structure, behave in a very different way in regard to light. It was pointed out above that a shoot grown in darkness forms very small etiolated leaves. The small size of the leaves clearly shows that the absence of light retards their growth.

Some bacteria have been found to move only when exposed to light. Movements of this kind which are directly due to light are included in what is known as the **phototonic effect of light.**

Lastly, the members of plants are more or less irritable to the *direction* of the light, and tend to grow either in the direction from which the light comes, when they are described as **positively heliotropic**, or in the opposite direction, when they are called **negatively heliotropic**; or the reaction may be such that the member arranges itself at right angles to the incident rays of light, when it is described as **dia-heliotropic.** In heliotropism, as in all the *mechanical* as distinct from the *chemical* effects produced by light, the active rays are those of high refrangibility. This may be demonstrated by using the double bell-jar shown in Fig. 197 (p. 414), which must be covered so that light can pass in through a slit on one side only; or a more convenient arrangement is to make a cardboard or wooden box, which is blackened inside and provided with a narrow slit in one wall through which the light (which may be either white or coloured) is admitted. Mustard seeds are germinated in darkness in a small pot, and when the hypocotyls are about an inch long, the pot is placed in the prepared box or jar, into which white light is allowed to pass from the slit. In a few hours it will be found that all the shoots are turned towards the light, i.e. they are positively heliotropic, while the seed-leaves are arranged with their surfaces at right angles to the incident light, i.e. they are dia-heliotropic. If the light entering into the box passes through a coloured medium, so that only red or yellow light falls on the plants, no heliotropic curvatures will be induced. Speaking generally, both primary stems and primary roots tend to grow so that their

long axes lie in the direction of the brightest incident light, but the direction of growth in length is of course opposite in the two cases. In the case of a stem, as the irritability to the direction of light is only manifested in the growing region, the final position taken is a fixed one—**the fixed light position.**

The negative heliotropism of roots is well seen in the clinging aërial roots of the ivy. Of course a number of influences come into operation in determining the direction taken by a subterranean root besides heliotropism, e. g. variation in the amount of moisture in different parts of the soil will prevent a root from growing vertically downward.

The dia-heliotropic position of most leaves (those with dorsi-ventral structure) is fixed during growth ; it is such that the ventral surface of the leaf is directed towards the source of light, and so receives the maximum amount of light. This direction is not necessarily horizontal, nor will all the leaves on a plant have the same position with regard to the direction of strongest incident light. Some plants even put their leaves in a vertical position with the leaves facing east and west, so that both surfaces are about equally exposed to light.

The Influence of Gravity on the Direction of Growth of Plants (Geotropism).

It has been found that gravity exercises an important influence on the direction of growth of most plant members. Primary roots, for instance, commonly grow downwards in the direction of the centre of the earth, and are said to be **positively geotropic.** It must be clearly understood that this direction of growth in a root is not merely the result of its weight, of its negative heliotropism (p. 469), or of the search for water (p. 472), but is partly due to its irritability to the stimulus of gravity. That this is so may be demonstrated by experiment. Germinate some bean seeds in damp sawdust and select one with a strong straight primary root about 1 or $1\frac{1}{2}$ inches long, and fix it by pins passed through the cotyledons so that the root is horizontal and lies a short distance above the surface of some mercury contained in a shallow dish. The root should also be marked with lines or dots as is done in the experiment on the localization of growth (p. 463). The apparatus should now be covered over and kept in the dark for some hours, and the root-tip will then show downward curvature into the mercury owing to its positive geotropism. This curvature cannot be due to the influence of light as the plant has been kept in darkness ;

it is not due to moisture; and the fact that it is not due to mere weight is shown by its growing downwards into the mercury so as to displace very much more than its own weight of that heavy liquid. Examination of the lines or dots made on the young root should show that the curvature is confined to the growing region, i.e. that the part behind the growing region is incapable of responding to the stimulus.

Young stems show similar geotropic curvature, excepting that it takes place in the opposite direction, i.e. away from the centre of the earth. This **negative geotropism** may easily be seen in young grass seedlings. Germinate some barley in moist sand or earth, and when the shoots have grown about an inch in length, pull the plants out of the soil, and lay them down so that the shoots are horizontal. Keep them in the dark: in a day or two the shoots will be found to be growing vertically upwards. The part that had ceased to grow at the time the experiment was started remains in the horizontal position.

That the curvature of the stem is really due to the influence of gravity may also be demonstrated by placing a plant under such conditions that the directive influence of gravity can have no effect, and showing that no curvature then takes place. The most convenient way of doing this is by using an instrument known as a **clinostat**, which consists essentially of a clockwork arrangement by which the plant can be kept in a state of slow rotation. A plant (in a pot), the stem of which naturally grows vertically upwards, is fixed to the clinostat so that the stem is horizontal; the clockwork is then set in motion so that the plant is caused to rotate slowly about its longitudinal axis. No curvature takes place if the plant is kept in the dark; this is because the stimulus being received by each side of the growing point in succession (and not by the lower side only as would be the case if the plant were in the horizontal position but not in rotation), there is no reason why the stem should curve to one side rather than another, and so it grows straight outwards.

Some members, especially those with dorsi-ventral structure, such as most leaves, are **dia-geotropic**, and arrange themselves so that their longitudinal axes are horizontal. Such members are also dia-heliotropic (p. 469), and the more or less horizontal position assumed is the result of the influence of both light and gravity.

Some members with radial structure, such as rhizomes, are also dia-geotropic, as are also some flowers. A good example of a dia-geotropic

flower is seen in *Narcissus poeticus*, the flower of which commonly stands nearly at right angles to the vertical scape on which it is borne; if such a flower is so placed that it is out of the horizontal, it will at once begin to curve so as to get into that position.

Geotropic curvature does not take place in the absence of oxygen. This may be demonstrated by suspending some seedling beans in two bottles so that the young roots are horizontal. One bottle contains only a little water at the bottom, while the other is filled with boiled water sufficient to cover the seedlings. In a few hours the roots of the seedlings suspended in moist air will show downward curvature, while those in the water remain straight. If the water is afterwards removed, the roots soon show the characteristic curvature.

The Influence of Variation in the Degree of Moisture on Direction of Growth (Hydrotropism).

Ordinary roots show marked irritability to variation in the degree of moisture in the surrounding medium. To show this Sachs' experiment may be performed. Remove the bottom and the lid from a cigar box, so as to leave just the four side pieces. Some rather fine netting is then nailed on so as to make a perforated bottom, and a thin layer of moist sawdust is spread over the netting. Soaked barley grains are then laid on and covered with a thick layer of sawdust. The whole is suspended so as to make an angle of about 45° with the horizontal. The grains germinate and the roots grow through the meshes of the netting, but instead of growing vertically downwards, and so following their geotropic tendency, they curve so as to grow along the damp surface of the netting. Roots therefore show strong **positive hydrotropism**. This experiment is best performed in a greenhouse, as it is necessary for the air to be moist in order to keep the roots in a healthy condition.

Irritability to Sudden Variation in Temperature.

Some plants show marked irritability to sudden variation in temperature, even though the variation is but a few degrees. This form of irritability, in which variation in temperature acts as a stimulus, generally acts together with, and produces much the same effect as, variation in the intensity of light, i. e. fall in temperature is generally accompanied by diminution in the intensity of the light. But the reactions caused by variation in temperature may be induced at any time or in any

degree of illumination, so that they are really independent of the latter. The flowers of *Crocus* or tulip close with fall in temperature and open again when the latter rises. Both these flowers are sensitive to very small (2° or 3° C.) variations in temperature. Many plants showing 'sleep movements,' such as the wood-sorrel (*Oxalis*, p. 467), assume the night position even in the daytime if the temperature falls.

Movements due to Mechanical Stimuli.

Many plants exhibit movements of a more or less complex kind when they are touched or subjected to pressure, or when some special localized region, known as the **motile organ** (e. g. the pulvinus of a motile leaf, p. 467), receives the stimulus.

The movement so induced may have for its object the nutrition of the plant, as in the sundew (*Drosera*); it may aid in ensuring pollination, as in the irritable stamens of the barberry and the irritable stigma of the musk; it may assist the plant to climb, as is the case with the irritable tendrils of bryony, &c.

The movements of the tentacles of the leaves of the sundew have been already described (p. 424): it is interesting to note here that the movements induced by inorganic particles, such as grains of sand or small pieces of glass, only take place when the irritating particles actually touch the gland, i. e. it is not sufficient for them to simply lie in the drop of secretion. Nor does movement take place if any part of a tentacle other than the terminal gland is stimulated. Chemical stimuli as well as mechanical ones may cause inflexion of the tentacles. This plant also serves as a good example of the *transmission of stimuli from cell to cell and from tentacle to tentacle*; if only a few tentacles are directly stimulated, the disturbance is transmitted to the others, and after a time they all bend over towards the irritating insect or other object. It is probable that in this case the stimulus is carried from cell to cell by the connecting threads of protoplasm (p. 462).

Venus's fly-trap (p. 425) affords another example of irritability having the capture of insects as its object.

Tendrils afford other good examples of irritability to contact and pressure (see Figs. 5 and 7, pp. 15 and 17). These are specially modified branch or leaf structures; in the former case they generally bear small scaly leaves. The movements produced as a result of pressure are such as to cause the tendril to curve round the object with which it comes into contact, as is well seen in the vine and white bryony. Notice that

the effect produced by the stimulus is not confined to the part of the tendril which is actually in contact with the supporting object, but that the free portion of the tendril coils spirally, and so draws the plant nearer to the support. In some cases (e.g. some species of *Ampelopsis*), the tendril does not wind round the object, but simply fixes itself to an object, such as a brick wall, by a flat **attachment disc** which is formed at the stimulated apex.

If a tendril is examined it will be found to be somewhat curved or hooked at its end, and as a rule the irritability is localized to the concave surface of this hook. This fact can easily be demonstrated by rubbing one of the tendrils of the common bryony with a pencil; it will be found that stroking the upper (convex) surface produces little effect, but stroking the lower surface of the hook produces strong curvature in a few minutes.

In *Clematis* and *Tropæolum* (the so-called garden nasturtium) the petioles of the leaves are irritable to contact, and act much as tendrils do in some other plants.

Roots also exhibit irritability to pressure, such that they curve away from hard objects with which their growing apices may come in contact.

Some flowers also exhibit movement as a result of stimulation by mechanical means. The irritable stamens of the barberry will serve as a good example of this: the six stamens lie normally in a nearly horizontal position close to the petals, but when the outer surface of the base of the filament, or the inner surface just below the anther, is stimulated, each stamen rises on its point of attachment to a nearly vertical position. If the movement is induced by an insect (as is commonly the case) the result is that the anther probably strikes the insect and dusts it with pollen.

Another good example of an induced movement in a flower is afforded by the irrritable stigma of the musk (*Mimulus*). The stigma of this plant consists of two divergent lobes, the inner surfaces of which are very sensitive to contact; on being touched the lobes instantly close together, a movement which doubtless ensures the adhesion of pollen brought by an insect.

One of the best-known instances of mechanically induced movement is that shown by the sensitive-plant (*Mimosa*), which belongs to the *Leguminosæ*. A leaf of this plant consists of a primary petiole branching at its apex into four secondary ones, each of which carries pinnately-arranged leaflets (Fig. 227, III, p. 483, shows one of the

secondary petioles with its leaflets). The primary petiole is articulated to the stem, the secondary petioles to the primary one, and the leaflets to the secondary ones by special cushions of tissue, each of which is known as a pulvinus, and which serve as motile organs; and in the expanded condition the primary petiole stands out at a wide angle from the stem, the secondary petioles are well separated from one another, and the leaflets are spread horizontally. If the plant is shaken the primary petiole falls, the secondary petioles come closer together, and the leaflets move upwards and come together. A single leaflet may be made to move by stroking the lower side of its pulvinus, and the irritation thus set up will gradually travel to the other leaflets and cause them to close also, thus affording another example of the 'transmission of stimuli.' The movements are produced by changes in the turgidity of the parenchymatous cells of the pulvini, e. g. the main petiole sinks downwards because the cells of the lower portion of its pulvinus lose their turgidity as a result of the stimulus, and are no longer able to support the weight of the leaf.

PART IV

CHAPTER XXV

TECHNICAL DESCRIPTION OF PLANTS AND DEFINITION OF TERMS.

IT is very good and useful practice for the student, even from the very early stages of his study of botany, to write out descriptions of any plants which he can obtain. The great value of such work is that it compels him to observe for himself what otherwise he may only read about in books, and the fact cannot be expressed too emphatically that book-work alone in such a subject as this is practically useless, either as knowledge or as training in exact scientific method.

The members of the plant should be described in definite order; the usual and best plan is to start from below and work upwards, i. e. to describe the root first and the flower last. The beginner should endeavour to give as full and concise an account of each part of the plant as possible; the more advanced student will not only do this, but should, from his general knowledge, be able to give special attention to those features which are of *classificatory* importance, as the ultimate end aimed at during the description is generally the reference of the plant to its natural order, genus, and species.

A very large number of special technical terms are, or have been, employed in plant description; some of these are very useful and should be employed (provided their meanings are properly understood), as by their use we are enabled to express concisely (in one or a few words) what would otherwise take a long sentence; others, and there are a large number of such, are absolutely useless excepting for international purposes, as they merely express in Latin or Greek form what may just as well be given in easily understood English. The writers of the older botanical textbooks are responsible for the general opinion so often expressed, that botany is all long names; the less 'academic' treatment adopted by modern authors, by which the attention of the student is directed to the things themselves rather than to their names, cannot but be for the best.

The object to be aimed at, in writing a description of a plant, is to give such an account as would enable a botanist, even though he had never seen the plant, to place it in its systematic position, or if the plant is new to science, to refer it to the genus or species to which it is most nearly related.

In this chapter a scheme of classification will be given to show the order in which the members and their parts may be taken. Only the more important technical terms will be employed, and they will be accompanied by short definitions, or by references to the pages of the book on which such definitions will be found. This will be followed by simple descriptions of a few common plants, which the beginner will find it useful to compare with the plants themselves.

The Plant generally. The size of the plant and its general appearance should be noted: is it a *tree* (i. e. a tall woody plant with a main stem), a *shrub* (i. e. a woody plant which branches freely near the ground and is not more than twenty feet high), or a *herb* (i. e. a plant which either dies completely before the winter, or at least its above-ground parts do so)? Is it an *evergreen* (i. e. never devoid of leaves, because the leaves are not all shed at the end of the season); or are the leaves *deciduous* (i. e. all fall off at the end of the season)?

Is the plant an *annual* (i. e. a plant which runs through the whole course of its development up to the formation of seed in one year and then dies); a *biennial* (i. e. one which produces vegetative structures only during the first year, and flowers and seeds during the second year, then dies, e. g. the turnip); or a *perennial* (i. e. a plant which lives for several years and usually produces flowers and fruit many times)? A perennial plant may be *woody* (i. e. having woody persistent stems, with or without evergreen leaves, as in ordinary trees and shrubs), or *herbaceous* (i. e. all the above-ground parts die down in the winter, and fresh aërial stems, leaves, &c., appear during the next season). If the plant is a herbaceous perennial what enables it to perennate – a rhizome, tuber, bulb, corm, &c.?

The Root. Is the root-system well developed in proportion to the size of the plant, or is it scanty? Does it spread mainly in a vertical direction or in a horizontal one? Is there a *tap-root* (i. e. a distinct more or less fleshy main root formed by direct prolongation of the radicle of the embryo); or is the root *fibrous* (i. e. consisting of a number of approximately equally fine roots, as in grasses, in which the radicle of the seed does not usually elongate)?

If a tap-root is present its shape should be given—*conical* (e. g.

parsnip and carrot): *spindle-shaped* or *fusiform* (e.g. radish); *napiform* (e.g. turnip), &c.

Are all or any of the roots *adventitious* (i.e. arising from nodes of the stems, or from the leaf-stalks, or not in acropetal order on *roots*), or are they all *normal* (i.e. springing from other roots in acropetal order)?

Do any of the roots become thick, hard, and woody? Does the main root-axis serve as a storehouse of food-material and so become swollen or *tuberous*; or are there a number of such swollen rootlets as in the *Dahlia*, in which the root is also described as tuberous? The *root-tubercles* of *Leguminosæ* should be noticed and described (see p. 420). Roots are sometimes *aërial* (e.g. ivy, tropical orchids, &c.); if such roots are present anything special about them should be described, e.g. that the ivy climbs by means of them—that the aërial root of *Vanilla* (an orchid) is a tendril, &c.

Sometimes plants are *parasitic* by their roots and the roots will be found attached to those of another plant (see p. 423).

The Stem (and its branches). Is there a distinct main stem forming the ascending axis of the plant, and strong enough to stand erect and support the weight of branches, leaves, and flowers?—such a stem is described as *erect*; if it lies partially on the ground but rises above it at the end, it is *ascending*; if entirely on the ground, *prostrate*.

Stems may be *climbing* (by tendrils, as in the Virginian creeper; by roots, as in ivy; by twisting their leaf-stalks, as in *Clematis*; by hooked prickles, as in the bramble; &c.), or *twining* (i.e. twisting their stems round a support, as in honeysuckle and *Convolvulus*).

Branches may be developed as *runners* or *stolons* (i.e. lateral horizontally-growing branches formed just above the ground-level and bearing small scale leaves and adventitious roots; fresh aërial shoots are developed from some of the nodes, and finally, on the decay of the connecting runners, these form new plants); *suckers* (i.e. similar to runners but given off just below the surface of the soil, finally striking upwards and giving rise to a new aërial shoot); *offsets* (i.e. similar to the runners but shorter and producing only a single bud at the end, as in the houseleek); *tendrils*, as in the Virginian creeper, where the tendril bears scaly leaves, in the axils of which branch tendrils arise (Figs. 5 and 6, p. 15); *spines* (i.e. short pointed branches arising in the axils of leaves, and often themselves bearing small leaves, as in the hawthorn, Fig. 8, p. 17); *cladodes* or *phylloclades* (i.e. flattened branches with the same functions as foliage leaves, but shown to be

branches, (1) because they arise in the axils of small scale leaves, and (2) because they themselves bear scale leaves and flowers either on their upper or lower surfaces or on their edges ; examples are seen in the butcher's broom (Fig. 11, p. 18), some *Cactaceæ*, &c.

Some underground stems may be *rhizomes*, i. e. shoots which grow horizontally under the soil, and a characteristic feature of many herbaceous perennials. A rhizome may be long and thin as in sedges, or thicker and fleshy as in Solomon's seal; it may be *monopodial*, in which case the annual aërial shoots develop from buds in the axils of the scale leaves on the rhizome, as in the wood-sorrel; or *sympodial*, as in Solomon's seal, where the end of the rhizome itself bends upwards and develops into the aërial shoot, while the subsequent elongation of the rhizome is effected from a lateral bud. Underground stems may also be *corms*, i. e. short, thick, fleshy stems covered with scaly leaves. The corm of the *Crocus* has usually a single bud at its apex from which the flowering shoot of the current year arises, while the corm from which next year's shoot will be developed is formed by swelling of the lower part of the current year's aërial shoot: the corm of *Gladiolus* (Fig. 13, I, II, p. 19) is similar, but the corm of next year is formed from a lateral bud near the depressed apex from which the current year's shoot arises, while a number of accessory buds are also formed which may separate and give rise to new plants: the corms of *Colchicum*, instead of developing upwards as in *Crocus* and *Gladiolus* (in which the corm of the current year lies on top of the shrivelled remains of that of the last), develop laterally so that the successive corms lie side by side; this is owing to the fact that the new corm arises from a lateral bud developed *low down* on the old corm. Underground stems may also be *tubers*, i. e. swollen subterranean shoots bearing small scaly leaves with buds in their axils, as in the potato, in which the tubers are borne on slender white subterranean branches; the 'eyes' are the buds ; or *bulbs*, i. e. large buds with fleshy leaves covering a flattened stem, with adventitious roots on the lower surface. The bulbs of the onion and hyacinth (Fig. 13, V, VI) are described as *tunicate bulbs* because the fleshy leaves completely invest one another; that of the lily (Fig. 13, III, IV), in which the fleshy leaves merely overlap at the edges, is said to be *scaly* or *imbricate*.

Other details to be described in connexion with the stem are :—

Its *colour* and *outline in section*—whether *round* or *square*, *flattened*, *triangular*, *ribbed*, &c., and the relation of this to the arrangement of the leaves; whether the internodes are *solid* or *hollow* as seen by

cutting the stem (internodes) across, when it may also be possible to see the arrangement of the vascular bundles, i. e. whether they are in a single ring or scattered; whether the stem is perfectly free from hairs (*glabrous*) or hairy—in the latter case whether the hairs are soft or stiff, coarse or fine, long or short, or arranged in definite lines as in some species of *Veronica*. Special kinds of *hairs*, which are outgrowths of epidermal cells, or *emergences* that are outgrowths developed not only from the epidermis but from some of the deeper layers of cells as well, may be present and should be described; such are *prickles* or emergences as in the rose, *branched hairs*, *peltate hairs*, *glandular hairs* or those with expanded apices containing resin, mucilage, &c., and *stinging hairs* supported on basal cushions as in the stinging-nettle.

The Leaves. Whether *opposite*, *alternate*, or *whorled*; if opposite are they also *decussate* (i. e. does one pair of leaves alternate in position with the pair above or below, so that if in one pair the leaves lie at the front and back of the stem, those of the pairs above and below lie on the sides or right and left?), or are the successive pairs placed above one another or *superposed*; if the leaves are alternate how many vertical rows (*orthostichies*) do they make on the stem; if the leaves are whorled how many are there in each whorl—are they all alike an does each bear a bud in its axil?

Are the leaves *cauline* (i. e. arising from a distinct stem or stems), or are some or all of them *radicle* (appearing to come from the root, but really arising laterally on a very short stem at the ground level)?

Are they *sessile* or *petiolate* (without or with a leaf-stalk or petiole), *simple* or *compound*, relatively large or small?

Are they thin and green in colour (*herbaceous*), brown or pale in colour and small (*scale leaves*), or thick and fleshy (*succulent*), or rather thick, green, and leathery in texture and persistent (*evergreen*)?

According to the degree of lobing or incision a simple leaf may be *pinnately* or *palmately lobed*; it is the former when the incision is not deep and when the main veins and lobes are arranged on each side of the midrib; it is the latter when there is no distinct midrib, but a number of main ribs radiate out from the base of the lamina like the fingers of a hand; it is *pinnatifid* or *palmatifid* (Fig. 225, I) when the incision is about halfway to the middle of the leaf; *pinnatipartite* or *palmatipartite* when the incision is still deeper, as in Fig. 225, III; *pinnatisect* or *palmatisect* when the incision is *very* nearly to the midrib or to the base of the leaf, so that the leaf is almost a compound one.

If the leaf is a simple one, what is the outline or shape of the lamina (see Fig. 226)? The following are the principal forms: *acicular* or *needle-like* (as in the pine, Fig. 226, X); *linear* (when flat, long, and narrow, with parallel sides, as in grasses, Fig. 226, IV); *lanceolate* (when narrow, but broadest near the centre, as in the ribbed plantain, Fig. 226, III); *oval* (similar to lanceolate, but relatively shorter and broader, Fig. 226, I); *ovate* (similar to the last, but the greatest breadth near the base); *obovate* (with the greatest breadth near the apex, Fig. 226, VIII); *spathulate* or spoon-shaped (as in the daisy); *orbicular* (when the outline approximates to circular, Fig. 226, VI); *cordate* or heart-shaped (when the apex is pointed and the base indented, Fig. 226, VII); *obcordate* (when the reverse is the case, Fig. 226, IX); *auriculate* or *eared* (when the base of the lamina forms two ear-like outgrowths directed outward); *sagittate* or arrow-head shaped (when the two outgrowths are directed backward, e.g. sorrel, Fig. 194, I, p. 409). It is frequently found that a particular leaf does not conform to any one of these types but is intermediate between two of them; it may then be described as ovate-lanceolate, &c.

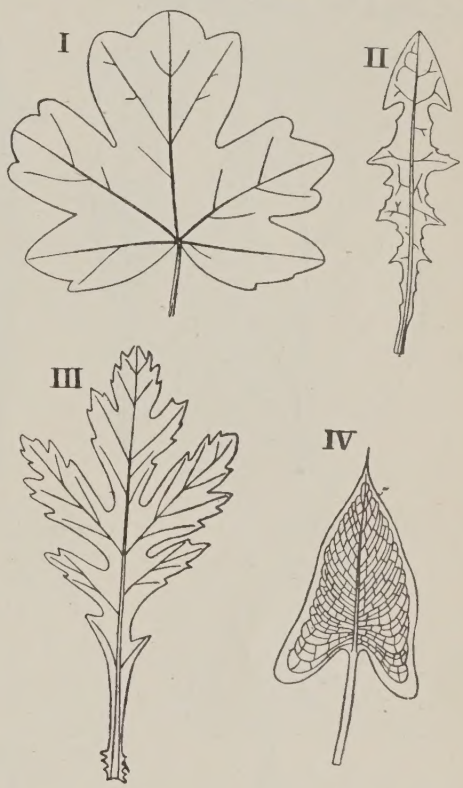


FIG. 225. Forms of leaves. I. Palmatifid leaf of Maple. II. Leaf of Dandelion. The lateral lobes are directed backward (runcinate). III. Pinnatipartite leaf of Marguerite. IV. Sagittate (arrow-head shaped) leaf of *Arum*.

What is the character of the apex of the leaf? It may be *rounded* or *obtuse*; *acute* (pointed); *acuminate* (when drawn out into a long tapering point); *mucronate* (when only the midrib projects); *emarginate* (when the apex is depressed; see Fig. 226, IX).

The margin of the leaf should be described. Is it *serrate* (i. e. with teeth directed forward as in Fig. 226, VII), *dentate* (i. e. with pointed teeth directed outwards), *crenate* (i. e. with rounded, not pointed, prominences as in Fig. 226, V), or *entire* (i. e. without teeth or prominences of any kind as in Fig. 226, II, III, IV)?

Is the lamina *net-veined* (*reticulate venation*) or *parallel-veined* (*parallel venation*), and what is the arrangement of the main veins (*pinnately* or *palmately veined*)?

If a compound leaf, what is the number of the leaflets and are they arranged *pinnately* or *palmately*? A compound leaf with three leaflets is called a *ternate* leaf (Fig. 227, II). The outline, apex, margin, venation, &c., of the leaflets should be described in the same terms as are used for a simple leaf.

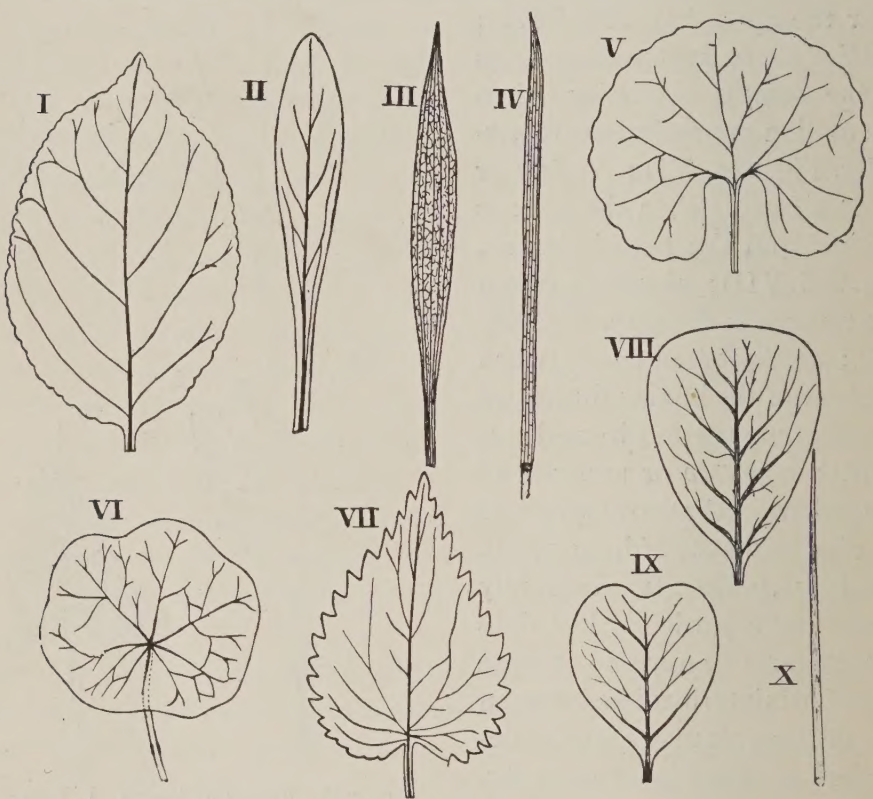


FIG. 226. Simple leaves. I. Outline oval; apex acute; margin crenate (Apple). II. Outline spathulate; apex rounded; margin entire (Stock). III. Outline lanceolate; apex acuminate; margin entire (Plantain). IV. Linear lamina of a Grass leaf. V. Outline reniform; margin crenate; apex obtuse. VI. Peltate leaf of *Tropæolum*. VII. Cordate leaf of Nettle. Apex acute; margin serrate. VIII. Obovate leaf. IX. Obcordate leaf. Apex emarginate. X. Acicular (needle-shaped) leaf.

All the leaves of the plant should be examined, as the lower leaves often differ markedly from the upper ones on the same stem.

The base of the leaf should be carefully examined; it may be expanded; it may sheathe the stem; it may extend for some distance down the stem (*decurrent*), or its two lobes may extend round the stem and meet so that the stem appears to pierce the leaf (*perfoliate*).

Is the leaf *stipulate* or *exstipulate*? If the former, the size, shape, persistence, &c., of the stipules should be carefully described (see Figs. 183, 194, 224, 227).

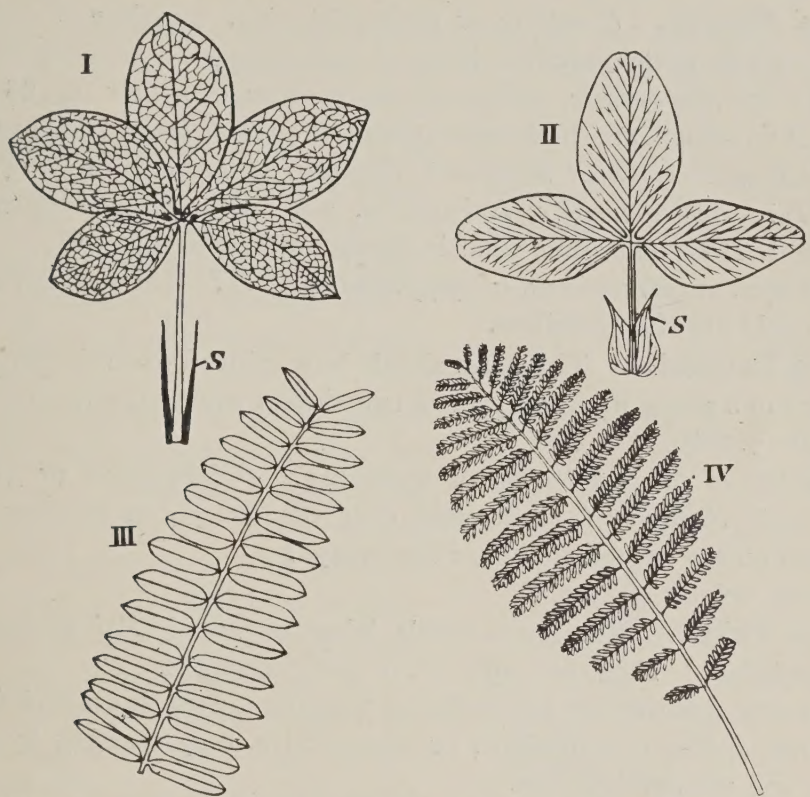


FIG. 227. Compound leaves of *Leguminosæ*. I. Palmate leaf of Lupin. S = stipules. II. Ternate leaf of Purple Clover (*Trifolium pratense*). S = stipules. III. Paripinnate leaf of *Mimosa* (only one-fourth of the complete leaf is shown). There is no terminal leaflet. If there is a single terminal leaflet the leaf is imparipinnate. IV. Bipinnate leaf of *Acacia*.

The presence or absence of hairs should be described as in the stem; sometimes long silky hairs are developed from the margin of the leaf, as in the beech, when the leaf is described as *ciliate*.

The Inflorescence. Are the flowers solitary or grouped? In either case the single flower or the inflorescence is described as *terminal* (i.e. terminating the *main* axis), or *axillary* (*lateral*). Is it *definite* or *indefinite* (p. 298). The kind of inflorescence (*raceme*, *spike*, *cyme*, &c., pp. 299–305).

Are all the flowers of the inflorescence alike? If not, describe the differences—they may differ in size, or the outer ones may be *neuter* (p. 27), *zygomorphic* (p. 297), &c.

Any special features should be described.

The Bracts. *Bracteate* or *ebracteate*? If bracts are present they should be described as to size, colour, shape, &c. How do the bracts differ from the ordinary foliage leaves?

The Flower. *Complete* or *incomplete* (i. e. complete if dichlamydeous and hermaphrodite, incomplete if mono- or achlamydeous) (p. 23)? *Hermaphrodite*, *unisexual*, *polygamous*, or *neuter* (pp. 23 and 27)? If unisexual, are the flowers *staminate* or *pistillate* (p. 283) and is the plant *monœcious* or *diœcious*? *Symmetry*: *regular* or *irregular* (p. 297)? *Actinomorphic*, *isobilateral*, *zygomorphic*, or *asymmetric* (p. 296)? If zygomorphic, what is the zygomorphism due to?

Hypogynous, *perigynous*, or *epigynous* (p. 287)? The size, perfume, &c., should also be described.

The Perianth. This term should be employed when the perianth consists of a single whorl only, or of two similar whorls (as in *Liliaceæ*) (see also p. 289).

Number of distinct leaves or segments? *Polyphyllous* or *gamophyllous*? *Superior* (i. e. inserted over the ovary), or *inferior* (i. e. inserted on the receptacle below the ovary)?

Shape, colour, texture, &c.

The Calyx. Number of sepals, lobes, or teeth? *Polysepalous* or *gamosepalous*? *Superior*, *inferior*, or *perigynous*?

Examine a flower bud and make out whether the sepals are *imbricated* (i. e. overlapping one another), or *valvate* (i. e. only meeting by their edges and not overlapping).

If there is an odd number of sepals, is the odd one anterior or posterior (p. 294)? How are the sepals arranged on the receptacle—are they in one or in more whorls or spirally arranged?

Are the sepals *green*, *petaloid* (i. e. any bright colour other than green), or *membranous* (i. e. small, thin, and dry)? One or more of the sepals may be *spurred*, or *saccate* (i. e. expanded at the base, as in the wallflower).

What is the persistence of the sepals? Are they *caducous* (i. e. falling off as the flower opens, as in the poppy); or *deciduous* (i. e. remaining on the open flower, but not persisting for the fruiting stage); or *persistent* (i. e. forming part of the fruit, as in the foxglove)?

When, as in the bulbous buttercup (*Ranunculus bulbosus*), the sepals are bent right back to the pedicel below the flower, they are described as *reflexed*.

If the calyx is polysepalous, the shape (outline), apex, colour, hairiness, number of distinct veins, &c., of a single sepal should be described;

if gamosepalous, its general shape should be given (*tubular* or *cylindrical*, *bell-shaped* or *campanulate*, *urn-shaped* or *urceolate*, *lipped* or *labiate*, &c.).

The calyx may be represented by a *pappus*. An *epicalyx* (Fig. 152, III, p. 284) may be present; if so the number of its leaves should be given.

The Corolla. Many of the terms used correspond with those used for the calyx.

Number of petals, lobes, or teeth?

Polypetalous or *gamopetalous*? *Hypogynous*, *perigynous*, or *epigynous*?

The arrangement of the petals in the bud (*æstivation*) may be *imbricate*; *valvate*; *contorted* or *twisted* (as in the petals of the mallow); *vexillary* (as in petals of the pea); or *crumpled* (i.e. when the petals are irregularly crushed together, as in the poppy).

How are the petals arranged with reference to the sepals—do they *alternate* with them or are they *superposed*? If there is an odd petal is it anterior or posterior in position?

If the petals are whorled how many whorls are there?

Petals are usually *deciduous* (p. 484). They may be *sepaloid* (i.e. green and like sepals); *membranous*; *spurred*; *saccate*; *reflexed*, &c.

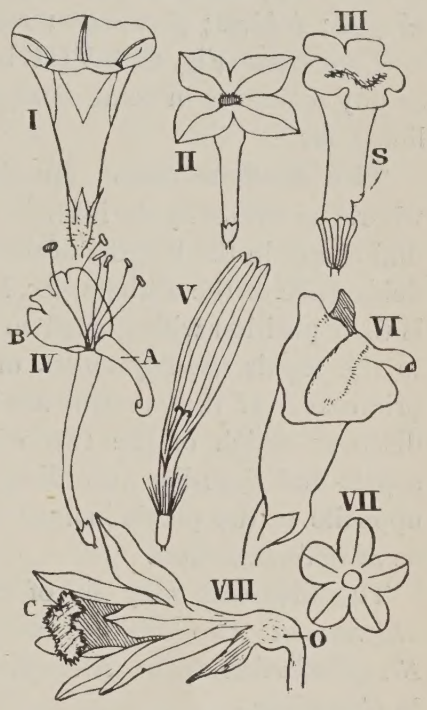


FIG. 228. Forms of gamopetalous corollas. I. Flower with funnel-shaped corolla. II. Flower of Lilac with hypocrateriform corolla. Differs from rotate (VII) in the possession of a long tube. III. Saccate corolla of Valerian. The sac (S) is really a short spur. IV. Flower of Honeysuckle with a lipped (labiate) corolla. A = lower lip representing one petal; B = upper lip representing four petals. V. Ligulate flower of a Composite. VI. Personate flower of Snapdragon. The lips are closed. VII. Rotate corolla of Elder. The tube is very short. VIII. Flower of Daffodil. C = corona; O = inferior ovary.

If the corolla is polypetalous, the shape, colour, &c., of a single petal should be described. Many free petals are *clawed* (i.e. they have a slender stalk or claw and an expanded spreading part known as the limb, as in many *Cruciferæ* and *Caryophyllaceæ*, Figs. 180, 181, pp. 361, 365).

Special names given to polypetalous corollas are *papilionaceous* (as

in the pea and bean); *cruciform* (as in *Cruciferæ*); *rosaceous* (i. e. with five free spreading petals without claws, as in the rose); *caryophyllaceous* (i. e. with five free petals with long claws and spreading limbs, as in many *Caryophyllaceæ*), &c.

If the corolla is gamopetalous its general shape should be given, i. e. *tubular*, as in Fig. 188, II; *bell-shaped*, as in Fig. 190, I; *funnel-shaped*; *labiate*; *personate*; *rotate*; *ligulate*, &c. (see Fig. 228).

If a *corona* (Fig. 228, VIII) is present it should be described, as well as any scales (as in some *Boraginaceæ*), hairs, special marks (directing lines), &c.

The Andrœcium. Number of stamens? In one or in more whorls as shown by the insertion on the receptacle at different levels, by differences in the lengths of the filaments, by differences in the time of dehiscence of the anthers, &c.? If the stamens are in one whorl what is their position with regard to the sepals or petals: are they opposite to the sepals (*antisepalous*), or to the petals (*antipetalous*) as in the primrose? If the stamens are in two whorls (*diplostemonous*) try and discover which of the two whorls (outer or inner) is opposite the sepals and describe accordingly; if the outer whorl of stamens are opposite to the petals instead of to the sepals the flower is described as *obdiplostemonous*.

The filaments may be of different lengths so that the flower is *didynamous* (two long and two short stamens), as in most *Labiatæ* and *Scrophulariaceæ*; or *tetradynamous* (two short and four long), as in *Cruciferæ*.

Is there cohesion between any or all of the stamens? If the filaments are coherent describe as *monadelphous*, *diadelphous*, or *polyadelphous* (p. 290). If the anthers cohere describe as *syngenesious*. If the stamens are all free describe as *polyandrous*. What is the adhesion of the stamens? *Hypogynous*, *perigynous*, *epigynous*, *epipetalous*, or *epiphyllous*?

The Anther. Are all the filaments provided with anthers? Some may be *staminodes*. Anthers may be *sessile* (i. e. without filaments). What is the shape of an anther? Elongated, short, round, &c.? How many pollen chambers or loculi does the anther contain? Is it *four-chambered*, *two-chambered*, or *one-chambered*? How does the anther dehisce to liberate the pollen? Is it by *longitudinal* slits, by *transverse* slits, by *valves*, as in the barberry (Fig. 179, III), or by *pores*, as in the potato? Try to discover whether the anthers shed their pollen before the stigmas are ripe (*protandry*), or vice versa (p. 310).

Is the dehiscence such as to shed the pollen towards the centre of

the flower (*introrse*), or away from the centre of the flower (*extrorse*), as in the *Iris*? The dehiscence may also be by slits at the sides of the anther-lobes (*lateral dehiscence*).

Is there anything of special interest about the connective? Are the anther-lobes *parallel* or *divergent* (e. g. dead-nettle)?

Note any special outgrowths from the anthers, such as the prolongation of the connective above the anther as in the violet (Fig. 166, II, p. 313) and oleander, the staminal nectaries of the violet, the peculiar staminal outgrowths of the heath (Fig. 186, II, p. 386), &c.

How is the anther attached to the filament? It may be *adnate* (when the filament simply continues upwards and forms the connective, so that the anther is not sharply marked off from the filament); *basifixed* (when the anther is sharply marked off from the filament and the latter is attached to the base of the anther); *dorsifixed* (when the filament is inserted in the middle of the back of the anther); or *versatile* (when the dorsifixed anther is attached to a pointed filament so that the former readily swings about in the wind, as in grasses).

The Gynæcium. Number of carpels? Is there more than one stigma? If so the number should be given, unless they are very numerous as in many apocarpous flowers. The size, form (globular or *capitate*, as in the primrose; *pointed*; *hooked*, as in some species of violet, &c.), degree of hairiness, &c., of the stigma should be described. If there is no style the stigma is described as *sessile*.

The Style. The number, length (long or short), colour, form, &c., should be described. Is there any decided difference in length of the styles of different flowers (*heterostyly*, as in the primrose and purple loosestrife)?

The Ovary and Ovules. If there is more than one carpel, is the ovary *apocarpous* or *syncarpous* (p. 291)? If apocarpous, how are the carpels arranged on the receptacle, in whorls (*cyclic*), or spirally (*acyclic*)? Is the ovary *superior* or *inferior* (p. 288)?

How many chambers are there in the ovary (*unilocular*, *bilocular*, *trilocular*, *quadrilocular*, *pentalocular*, or *multilocular*)?

How many ovules are there? There may be one, few, or many in each chamber.

If there is one ovule, where is it attached? It may be *suspended* or *pendulous* from near the top of the ovary; or *basal* (i. e. standing up on the floor of the ovary). If there are many ovules, what is the kind of placentation? *Marginal* (i. e. when the ovary consists of a single carpel and the ovules are arranged along the ventral suture

of the infolded carpellary leaf, as in the pea and Christmas-rose); *parietal* (i. e. when the unilocular (bilocular in *Cruciferæ*) ovary represents more than one carpel and has the ovules attached to placentæ which run down the walls, as in the violet); *axile* (i. e. when the ovary consists of two or more loculi or chambers, and the ovules are attached to the central axis, as in the lily); or *free-central* (i. e. when the ovary is unilocular with the ovules attached to a central column, as in the primrose).

The Fruit. (See Part II, Chap. XIX.) *Simple*, *aggregate*, or *compound*? *Dry* or *succulent* (when ripe)? *Dehiscent* or *indehiscent*? If simple, dry, and indehiscent, it may be an *achene*, a *caryopsis*, a *cypsela*, a *nut*, a *single samara*, or a *schizocarp*. If a schizocarp, into how many parts does it split? Special kinds of schizocarp are the *double samara* (maple), the *regma* (Geranium), the *cremocarp* (*Umbelliferæ*), the *carcerule* (mallow), the *lomentum* (radish), &c. (see p. 319).

If the fruit is simple, dry, and dehiscent it may be a *follicle*, a *legume*, a *siliqua* or *silicula*, or a *capsule*. If a capsule, how does it dehisce? Is it by teeth, by longitudinal slits, by pores, by a transverse split right round the ovary (as in the *pyxidium* of the scarlet pimpernel), or other special way?

If the fruit is a capsule and dehisces by the formation of long slits, is the splitting *loculicidal*, *septicidal*, or *septifragal* (p. 320)?

If the fruit is simple and succulent it may be a *drupe*, a *berry*, or a *pome*. If a berry, is it *superior* or *inferior*; *one-seeded*, *few-seeded*, or *many-seeded*; *unilocular* or *multilocular*?

If an aggregate fruit, what is the nature of the individual fruitlets? Are they achenes, follicles, or drupes? Is the receptacle fleshy or dry?

The Seed. (See Part II, Chap. XIX.) The size, form (round, flattened, winged, &c.), colour, peculiar markings of the testa, &c., of the ripe seed should be described. Is it albuminous or exalbuminous?

Has the seed an aril or an arillode? This may be fleshy as in the yew and spindle-tree, wart-like as in the castor-oil plant, or it may consist of a tuft of hairs as in the willow and poplar.

The following is a 'schedule' to be used as a guide to the technical description of plants. As many plants as possible, preferably wild ones, should be examined, taking the parts in the order given, and writing the descriptions in the spaces provided. Teachers are recommended to have a number of such blank schedules printed on fairly large sheets of paper. The schedule given is filled in for the **Shepherd's Purse** to illustrate the application of the terms used. An example is also appended of the description of a plant (*Geum urbanum*) without the use of a schedule. Beginners are advised to procure specimens of these plants and to carefully compare them with the descriptions given.

SCHEDULE FOR PLANT DESCRIPTION.

Name of plant (Common and Botanical).	SHEPHERD'S PURSE (*Capsella Bursa-pastoris*).		
Stem.		**Leaves.**	
Herbaceous or woody	Herbaceous.	Opposite or alternate	Alternate.
Approximate length	½ to 2 feet.	Simple or compound	Simple.
Glabrous or hairy	Nearly or quite glabrous.	Sessile or petiolate	Sessile.
Branching	Freely branching.	Arrangement of principal veins	Midrib only conspicuous.
Shape of cross-section	Circular.	Shape of lamina	Lanceolate, auricled at the base.
Other special characters	Ribbed.	Margin	Nearly or quite entire.
		Apex	Pointed.
		Glabrous or hairy	Short hairs.
		Other characters	Radicle leaves larger, pinnately lobed.
Inflorescence.		**Flower.**	
Racemose or cymose	Racemose.	Complete or incomplete	Complete.
Kind	Simple raceme.	Symmetry	Isobilateral.
Bracteate or ebracteate	Ebracteate.	Regular or irregular	Regular.
Other characters		Other general characters	Small; white.

SCHEDULE FOR PLANT DESCRIPTION (*cont.*).

	No.	Cohesion.	Adhesion.	Other Characters.
Calyx. (Sepals)	4	Polysepalous.	Inferior.	In two whorls. Green.
Corolla. (Petals)	4	Polypetalous.	Hypogynous.	Small, white. Alternating with sepals.
Perianth. (Leaves)				
Androecium. (Stamens) Filaments Anthers	6	Polyandrous.	Hypogynous.	Tetradynamous.
Gynæcium. (Carpels) Ovary	2	Syncarpous.	Superior.	Spuriously biocular. Parietal placentation. Many ovules.

Fruit.		Other Characters of Fruit.
Dry or succulent	Dry.	Fruit triangular, notched at the top.
Dehiscent or indehiscent	Dehiscent.	Flattened at right angles to the false partition (angustiseptal).
One-seeded, few-seeded, or many-seeded	Many-seeded.	
Kind of fruit	Silicula.	

Class	Dicotyledons.
Sub-Class	Dichlamydeæ.
Series	Thalamifloræ.
Order	Cruciferæ.

Ordinal Characters and Formula.	Parts of the flower in twos and fours. Tetradynamous stamens, characteristic ovary and fruit. $K\,2, C \times 4, A\,2+2^2, G\,\underline{(2)}$.

DESCRIPTION OF A COMMON WILD PLANT

Herb-Bennet or Common Avens (*Geum urbanum*).

The Plant generally. A herbaceous perennial with erect branching stems 1–2 feet high. Perennating by means of a short rhizome.

Stem (aërial). Erect. Monopodial. Green in colour. Slightly hairy. Circular in section. Solid.

Leaves. Alternate. Cauline. Sessile. Lower leaves compound, consisting of larger segments and smaller ones pinnately arranged. Upper leaves merely three-lobed (palmatipartite) or without lobes.

Colour light green. Herbaceous.

Margin serrate.

Net-veined.

Principal veins of upper leaves palmately arranged.

Stipulate—large, leafy, serrated stipules.

Covered with white silky hairs.

Inflorescence. Terminal and axillary. Definite. Cyme, generally monochasial.

Flower. Complete. Regular. Actinomorphic. Perigynous.

Calyx. Sepals 5. Polysepalous and arising (with the petals and stamens) from the rim of a shallow cup formed by the receptacle, ∴ perigynous. Valvate in the bud. Odd sepal posterior. Green. Provided with a few long hairs on the lower surface. The sepals persist to the fruiting stage. There is an epicalyx of 5 small leaves.

Corolla. Petals 5. Spreading. Small. Polypetalous. Perigynous. Yellow. Alternating with sepals. Oval in shape, without claws (rosaceous).

Andrœcium. Stamens indefinite. Free (polyandrous). Perigynous. Anthers short; dark-brown in colour; two-lobed; dorsifixed; longitudinal dehiscence; introrse.

Gynæcium. Carpels indefinite. Apocarpous. Ovary superior. Styles notched. Ovaries hairy. One ovule in each ovary.

Fruit. An aggregate (or etærio) of achenes with long persistent hooked styles.

Class Dicotyledons. Shown by the stipulate net-veined leaves and by the parts of the flowers in fives. A lens shows the arrange-

ment of the vascular bundles of the stem in a single ring. The seed is exalbuminous and has two cotyledons.

Sub-Class Dichlamydeæ. Sepals and petals are present.

Series Calycifloræ. Petals free; petals and stamens perigynous.

Order Rosaceæ. Shown by the stipulate leaves; regular flowers; indefinite perigynous stamens; and apocarpous pistil.

Floral formula, K 5, C 5, A ∞, G $\underline{\infty}$.

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